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Current knowledge of trematodes (Platyhelminthes: Digenea, Aspidogastrea) in Chile

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Abstract: The aim of the present review was to evaluate the state of knowledge of trematodes (Platyhelminthes: Trematoda) in Chile, covering taxonomy, biology, geographic distribution, and a checklist of all taxa reported in the country. A total of 277 articles published between 1849 and December 2020, have been analyzed. A total of 215 taxa belonging to the subclasses Digenea and Aspidosgastrea have been reported from Chile, 119 of them identified to species level and only three species with completely described life cycles. Trematodes from Chile were found parasitizing both native and exotic species, however, no records from insects and most crustacean classes exist. Overall, 159 out of 3989 potential host native species were reported as hosts for trematodes. Molecular tools were used in more recent taxonomic studies. Although research on trematodes in Chile is on the rise, there is a clear need for more detailed taxonomic studies to include integrative taxonomy approach, deposition of helminths in collections and the training of new generation of parasitologists to better understand the diversity, ecology and evolutionary relationships of trematodes in the region.

Keywords: Trematoda, Digenea, Aspidogastrea, biodiversity, checklist.

INTRODUCTION

The class Trematoda is subdivided in two subclasses, Aspidogastrea and Digenea. The former group is small and comprises only four families, 12 genera and about 80 species (Roberts *et al*., 2013; Collins, 2017). On the other hand, digeneans are a very diverse group of parasites with more than 2500 genera and 18 000 nominal species (Kostadinova & Pérez-del-Olmo, 2014; Collins, 2017). However, there is a significant number of yet undescribed species, with some estimates suggesting that the total number of digenean species may exceed 44 000 (Carlson *et al*., 2020a).

Gay (1849) was the first to mention a trematode in Chile. It was a report of the liver fluke *Fasciola hepatica* (Fasciolidae) in cattle. Since then, trematodes have been reported from a variety of hosts across the country. Previously published checklists were restricted to particular groups of hosts or types of ecosystems (see Garín & González-Acuña, 2008; Muñoz & Olmos, 2008; Oyarzún-Ruiz & González-Acuña, 2021), while an overview covering the whole trematode fauna in the country is currently lacking. The aim of the present review was to analyze the data on trematodes in Chile and summarize of knowledge on their diversity, taxonomy, biology, and geographic distribution. We also outline the areas most urgently needing, attention and/or improvement in future research.

MATERIAL AND METHODS

Literature search

We performed an exhaustive bibliographic review of trematodes reported from domestic and wild animals, including humans, in Chile. Data from freshwater, marine and terrestrial environments, and all invertebrate and vertebrate hosts were included in this review. To achieve this objective, we analyzed 275 research articles, one book and one book chapter from physical libraries and electronic databases such as NCBI, ScholarGoogle, Scopus and Web of Science (WOS). The time cut-off for the published data was until December 2020. The present review did not consider "grey" literature (i.e. technical reports, conference proceedings, congress posters, theses) because they are not subjected to a peer review process.

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Taxonomy of hosts and parasites

The taxonomic classification for host species was stated as follows: AviBase (https://avibase.bsc-eoc.org/) for birds; FishBase (https://www.fishbase.in/search.php) for fishes; GBIF (https://www.gbif.org) and ITIS (Integrated Taxonomic Information System; https://www.itis.gov/), in this order of priority, for freshwater mollusks, reptiles, amphibians and mammals; and WoRMS (World Register of Marine Species; http://www.marinespecies.org/) and SeaLifeBase (https://www.sealifebase.ca/), in this order of priority, for marine mollusks and crustaceans. We followed Gibson *et al*. (2002), Jones *et al.* (2005), Bray *et al.* (2008), Roberts *et al* (2013), GBIF and WoRMS for the taxonomy of trematodes.

Hosts

The categorization of hosts as native, endemic, or exotic species followed Ministerio de Medio Ambiente (MMA, 2018a, b) and PNUD (2017). In addition, the diversity of native, endemic, and exotic animal species for every host group present in Chile was stated according to Valdovinos (1999), Martínez & González (2017), PNUD (2017) and Ministerio de Medio Ambiente (2018a, b; http://especies.mma.gob.cl).

Locations

The collection sites were attributed to Chilean regions represented by roman numbers and ordered according its geographical distribution from northern Chile to Chilean Patagonia following the Biblioteca del Congreso Nacional de Chile (BCN) (https://www.bcn.cl/siit/mapoteca/regiones) and Ministerio de Medio Ambiente (MMA) (2018a): (i) *Northern Chile*: XV= Arica y Parinacota region (18°22'4.8" S 70°13'1.199" W), I= Tarapacá region (20°9'49.202" S 69°32'46.841" W), II= Antofagasta region (23°36'14.873" S 69°5'3.401" W), III= Atacama region (27°33'25.842" S 70°0'56.477" W), IV= Coquimbo region (30°45'16.795" S 70°54'1.992" W); (ii) *Central Chile*: V= Valparaíso region (32°35'51.392" S 70°51'10.711" W), RM= Metropolitan region (33°30'13.172" S 70°45'44.692 W), VI= Libertador General Bernardo O'Higgins region (34°32'4.337" S 71°2'7.735" W), VII= Maule region (35°35'50.022" S 71°29'19.248" W); (iii) *Southern Chile*: XVI= Ñuble region (36°37'13.518" S 72°6'5.983" W), VIII= Biobío region (37°20'20.907" S 72°24'38.456" W), IX= Araucanía region (38°40'4.424" S 72°15'39.623" W), XIV= Los Ríos region (39°58'27.448" S 72°40'2.92" W), X= Los Lagos region (42°18'3.038" S 73°6'19.393" W); (iv) *Chilean Patagonia*: XI= Aysén del General Carlos Ibáñez del Campo region (46°28'16.16" S 73°31'14.417" W), XII= Magallanes y de la Antártica Chilena region (53°21'9.906" S 71°33'17.201" W).

RESULTS

Over the last 120 years, there is a clear tendency for the increase of number of publications reporting trematodes in Chile, with a first peak in the 1980s and a second peak in the 2010s (Fig. 1).

Trematodes

A total of 215 taxa of trematodes belonging to two subclasses, three orders, 47 families and 127 genera have been recorded in Chile. Of these, 119 (55.35 %; 119/215) taxa were identified to species level, with three species belonging to Aspidogastrea subclass and 116 to Digenea subclass (Table 1).

The most common digenean families mentioned for particular host groups were Fellodistomidae for mollusks, Microphallidae for crustaceans, Opecoelidae for fishes, Gorgoderidae for amphibians, Echinochasmidae and Echinostomatidae for birds, and Fasciolidae for mammals. Only family Opisthogonimidae was reported from reptiles.

Complete life cycles are known for only 3 out 119 species of trematodes reported in the country, namely *Fasciola hepatica*, *Proctoeces lintoni* (Fellodistomidae) and *Prosorhynchoides carvajali* (Bucephalidae).

Hosts

Trematodes were reported from 159 out of 3989 potential native animal species (including 14 out of 1081 endemic species) and 12 out of 92 exotic animal species known in Chile (Table 2). So far, there are no records of trematodes from insects or classes of crustaceans other than Malacostraca.

The highest diversity of trematodes was found in representatives of the following host orders: Mytilida (9 taxa) in mollusks, order Decapoda (3 taxa) in crustaceans, order Perciformes (75 taxa) in fishes, order Anseriformes (21 taxa) in birds, and orders Carnivora and Cetacea (7 taxa each) in mammals. One order of reptiles and one order of amphibians were reported as hosts.

Geographical distribution

Taxonomic diversity of trematodes at family level across different regions of Chile is presented in Figs 2-4. A total of 428 records were plotted for all trematode families. These records represent the sum of all taxa reported for every trematode family in every region of the country. Our analysis showed certain patterns in the distribution of several digenean families. For instance, families Allocreadidae, Brauninidae, Dicrocoeliidae,

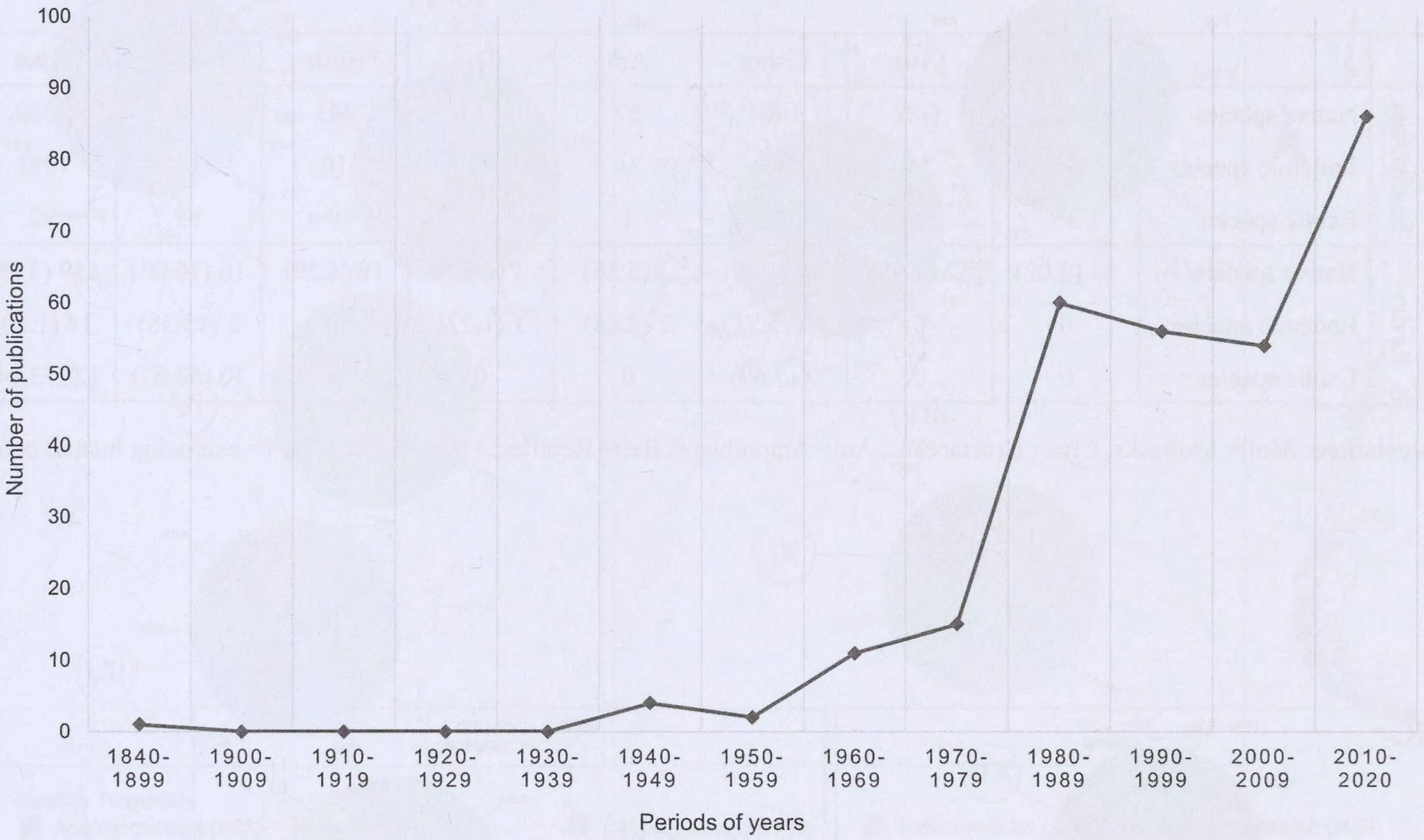

Fig. 1. Temporal tendendy in the number of publications related to trematodes in Chile.

Table 1. Parasitic taxa isolated from each host group.

	Moll‡	Crus	Fishes*	Am	Rep	Birds	Mam
Species	8	1	74	3	0	27	17
New species	3†	1†	22	3	0	0	3
Incompletely described	21	4	59	0	1	14	5
Genus sp.	7	0	49	0	1	11	4
Family gen. sp.	10	2	9	0	0	3	0
Subfamily gen. sp.	0	2	0	0	0	0	0
incertae sedis	4	0	1	0	0	0	1

Symbols and abbreviations: Moll= Mollusks; Crus= Crustaceans; Am= Amphibians; Rep= Reptiles; Mam= Mammals; ‡Including classes Gastropoda and Bivalvia; *including classes Actinopterygii, Holocephali and Elasmobranchii; †These species were also described from fishes.

Himasthlidae, Multicalycidae, Phaneropsolidae and Pleurogenidae have been recorded only in Southern Chile. Meanwhile, the Fasciolidae has been reported throughout the entire country.

The highest diversity of trematodes was recorded on Biobío region (VIII), Southern Chile, with 98 taxa belonging to 36 families, followed by Valparaíso region (V), Central Chile, with 62 taxa belonging to 20 families. On the other hand, the region with the lower diversity of trematodes was Libertador General Bernardo O'Higgins region (VI), Central Chile, with only 1 taxon (see Fig. 3).

Checklist

The checklist of the trematodes and their associated hosts is provided in the Appendix 1 [supplementary material S1]. The stage of development, parasitized organs, localities and references are also stated. An additional table provides a host-parasite list the Appendix 2 [supplementary material S1].

Table 2. Number of host species per host group in Chile (top 3 rows), and number and percentage, between parenthesis, of recorded species hosting trematodes in Chile (bottom 3 rows).

		Moll	Crus	Fishes	Am	Rep	Birds	Mam†	Total
Hosts biodiversity	Native species	1187	606	1401	57	135	443	160	3989
	Endemic species	886	21	35	34	82	10	13	1081
	Exotic species	35	0	26	1	2	9	19	92
Present Review	Native species	24 (2.02)	12 (1.98)	84 (6.00)	3 (5.26)	1 (0.74)	19 (4.29)	16 (10.00)	159 (3.99)
	Endemic species	0	0	9 (25.71)	2 (5.88)	1 (1.22)	0	2 (15.38)	14 (1.30)
	Exotic species	0	0	2 (7.69)	0	0	0	10 (52.63)	12 (13.04)

Abbreviations: Moll= Mollusks; Crus= Crustaceans; Am= Amphibians; Rep= Reptiles; Mam= Mammals; †= excluding human being.

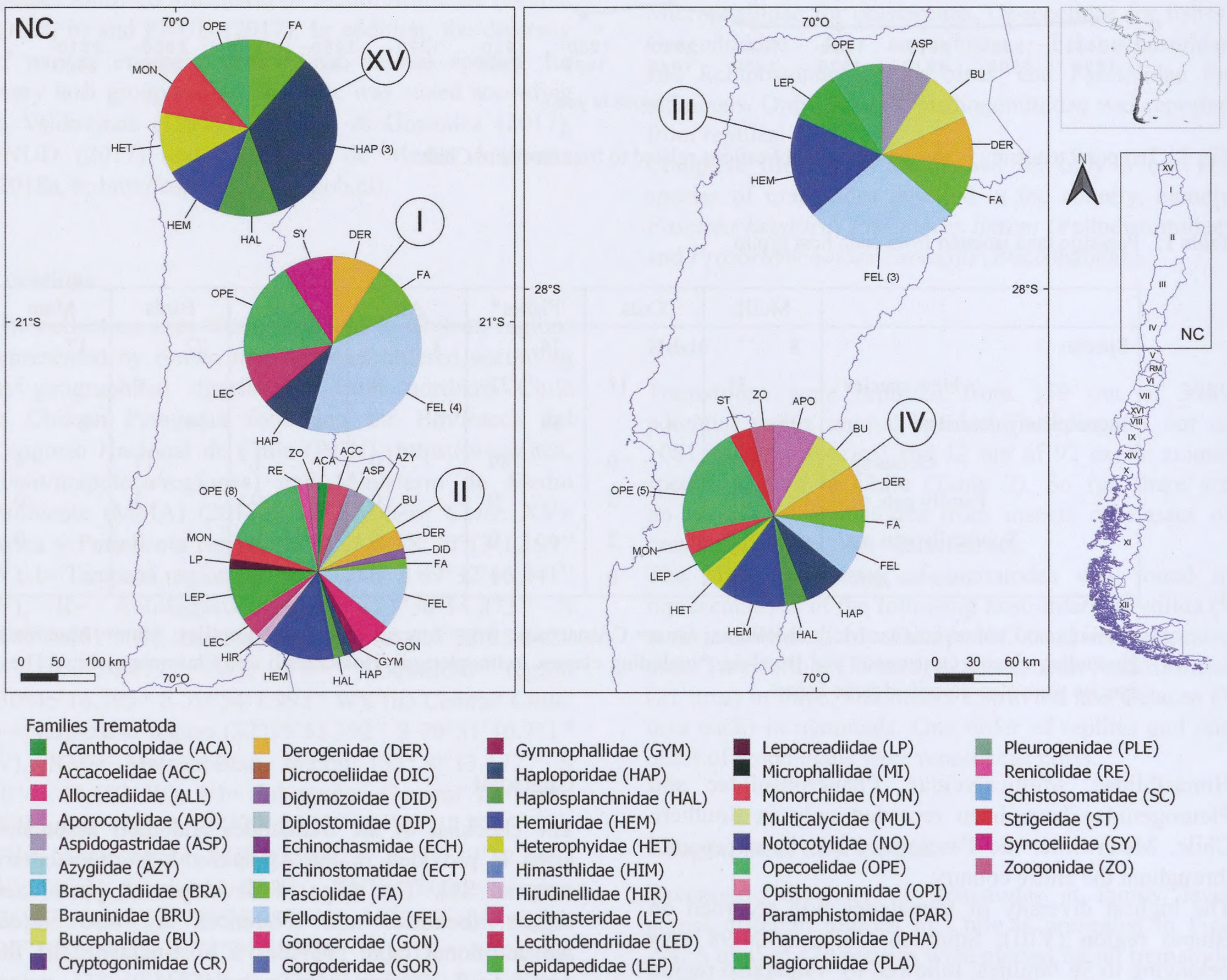

Fig. 2. Number of taxa per trematode family in Northern Chile (NC). Every color in the pie chart represents a particular family. The highest number of taxa for trematode families in every region is given between parentheses. The name of every region represented as a roman number is detailed in Material and Methods.

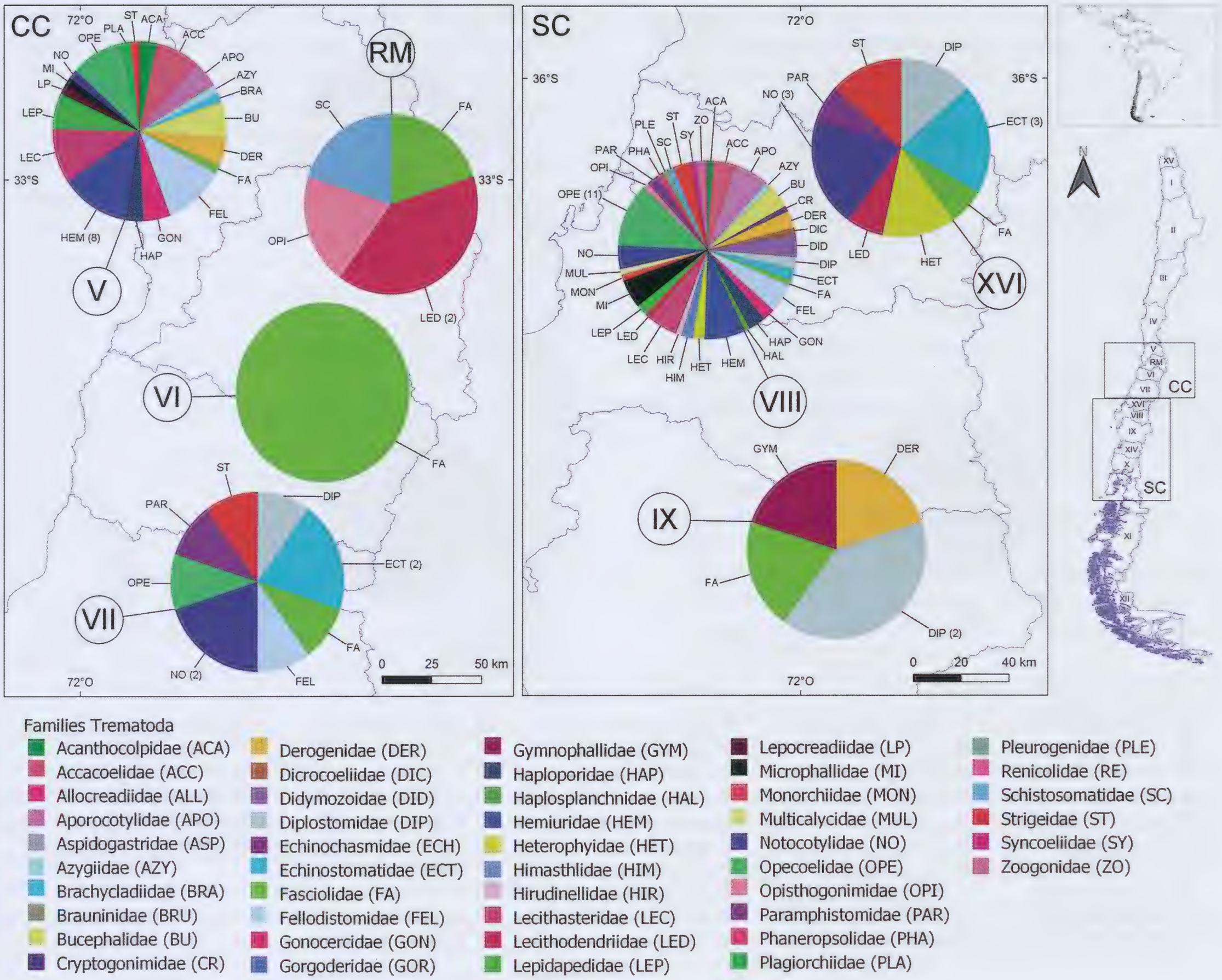

Fig. 3. Number of taxa per trematode family in Central Chile (CC) and Southern Chile (SC), regions XVI, VIII and IX. Every color in the pie chart represents a particular family. The highest number of taxa for trematode families in every region was stated between parentheses. The name of every region represented as a roman number is detailed in Material and Methods.

DISCUSSION

A significant trematode diversity has been recorded from Chile since the first publication by Gay (1849). However, the identification of a number of reported taxa is questionable, therefore, the collection of new quality specimens as well as the thorough re-examination of specimens deposited in museums are necessary. A number of species reported from Chile do not have descriptions or illustrations. For instance, *Proctoeces lintoni* (Fellodistomidae) (originally described from Europe) was reported in native fishes from Chile without adequate descriptions (Valdivia *et al*., 2010; Oliva *et al*., 2018). In the absence of DNA sequence data, comparisons with the two native species from Chile, *P. humboldti* and *P. sicyases*, is not possible (George-Nascimento & Quiroga, 1983; Valdivia *et al*., 2010; Oliva *et al*., 2018). Taking into account the uncertainty of the identification, the information on life cycle and presence of *P. lintoni* in Chile should be considered with caution (Valdivia *et al*., 2010; Oliva *et al*., 2018). The same is true for *Helicometrina nimia* (Opecoelidae), another European fluke reported in Chile, which needs additional analysis to establish its identity (Oliva *et al*., 2015).

Although complete life cycles are known for only 3 species of digeneans reported from Chile, larval stages of some other species have been reported. For instance, metacercariae of *Stephanoprora uruguayense* (Echinochasmidae), parasitic as an adult in seabirds, have been reported from two native fish species (Torres *et al*., 1982, 1983, 1991, 1992a, 1993a, 2017; Viozzi *et al*., 2008). Although in Chile the first intermediate host of this digenean remains unknown, aquatic snails of family Hydrobiidae have been recorded as its first intermediate host in Argentina (Ostrowski de Núñez, 2007). Members of family Hydrobiidae are distributed in Chile (Valdovinos, 1999), therefore, we anticipate that

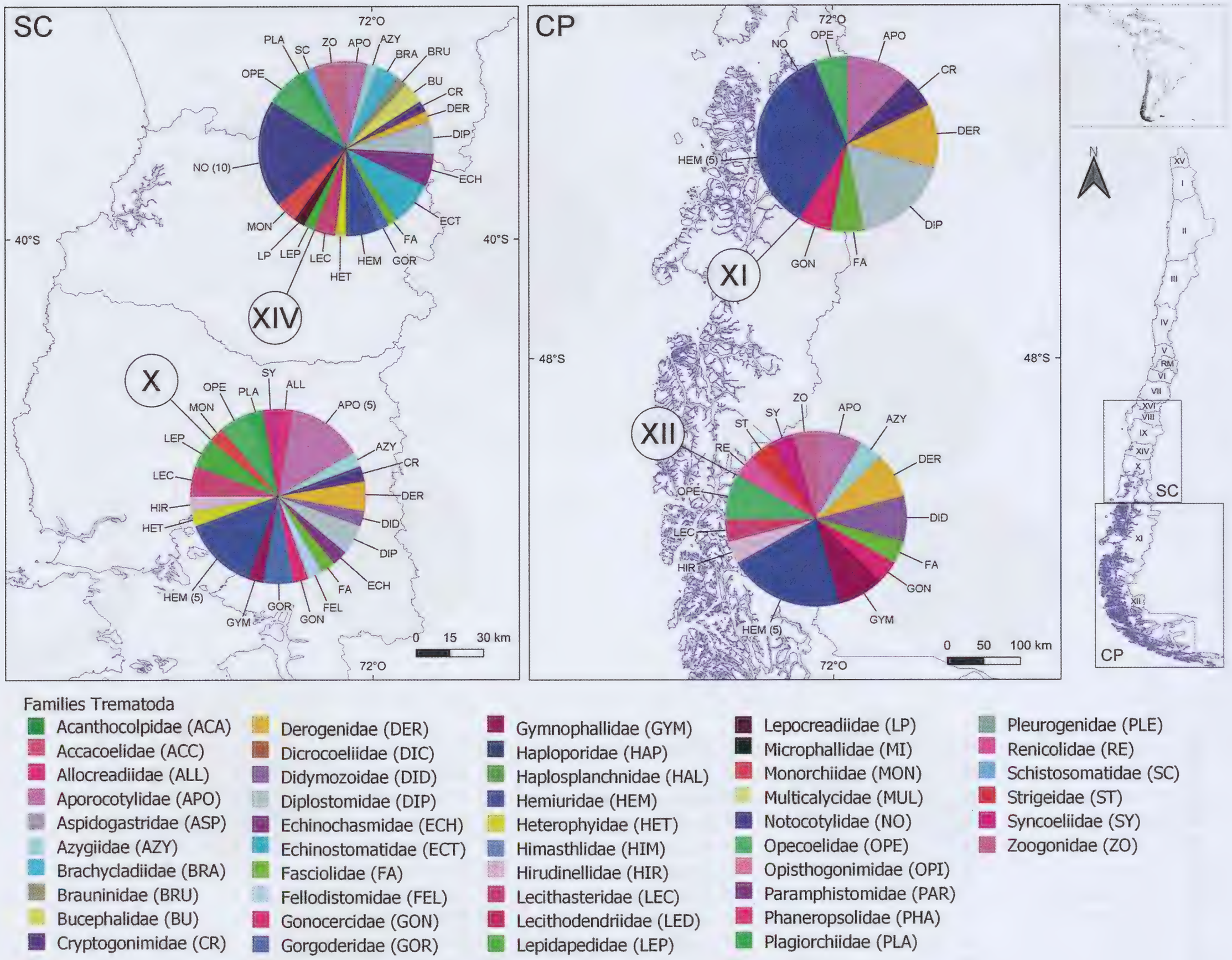

Fig. 4. Number of taxa per trematode family in Southern Chile (SC), regions XIV and X, and Chilean Patagonia (CP). Every color in the pie chart represents a particular family. The highest number of taxa for trematode families in every region was stated between parentheses. The name of every region represented as a roman number is detailed in Material and Methods.

future surveys may reveal the local transmission pathway of this trematode.

The insufficient coverage of host species diversity by parasitological studies in Chile (see Garín & González-Acuña, 2008; Muñoz & Olmos, 2008; Oyarzún-Ruiz & González-Acuña, 2021) might underestimate the complete richness of trematode species in the country. This echoes the situation of the coverage of South American fishes by parasitological studies with only 5 % of their total diversity examined for parasites so far (Choudhury *et al*., 2016).

Among introduced animals, cattle, and lagomorphs have been reported as hosts of *F. hepatica* (e.g. Alcaíno & Gorman, 1999; Courtin *et al*., 1975, 1979; Oyarzún-Ruiz *et al*., 2019b), and some salmonid fishes were reported as hosts of digeneans (Arata *et al*., 1977; Torres, 1995; Torres *et al*., 1992a). While publications on the helminth fauna of other exotic species such synanthropic rodents (*Rattus rattus*, *Rattus norvegicus,* and *Mus musculus*) do exist, there are no records of trematodes on these vertebrates (see Rojas *et al*., 1971; Landaeta-Aqueveque *et al*., 2014, 2018; Seguel *et al*., 2017).

Only a small proportion of studies on trematodes in Chile were performed using experimental infections (e.g. Tagle, 1944; Fernández, 1987b; Rebolledo *et al*., 2014; Muñoz *et al*., 2015). Thus, authors want to emphasize the need for performing this kind of studies, because these would help to a better understanding of the relationships between parasites and their hosts, mechanisms of transmission, pathological changes, behavioral manipulation, among others (Fried, 2000; Ostrowski de Núñe *et al*., 2004; Morley & Lewis, 2014; Blasco-Costa & Poulin, 2017; Karvonen *et al*., 2017).

The present review highlights the clear need for the broader use of molecular tools in the taxonomic studies of trematodes in Chile. Although the first study using DNA sequencing was published in 2010 (Valdivia *et al*., 2010), the number of works applying molecular techniques is

still limited. The combined use of morphological and molecular approaches (aka integrative taxonomy) is the most promising approach to advance our knowledge of biodiversity, classification, diagnostics, and phylogenetic interrelationships of trematodes and other parasites (Kostadinova & Gibson, 2000; Kostadinova & Pérez-del-Olmo, 2014; Hoberg *et al*., 2015).

Another interesting and currently discussed topic is the conservation of parasites (Gómez & Nichols, 2013; Carlson *et al*., 2020b). Some trematodes reported in Chile have been found in endemic species, e.g. *Gorgoderina valdiviensis* (Gorgoderidae) in the helmeted water toad (*Calyptocephalella gayi*) (Puga, 1979, 1982) and *Rudolphitrema chilensis* (Plagiorchiidae) in the rosy ground frog (*Eupsophus roseus*) (Puga, 1986; Puga & Torres, 1999), with no additional reports in other hosts (see Fernandes & Kohn, 2014). In addition, hosts of these particular flukes are considered threatened species with declining populations (IUCN, 2020). Considering their host specificity, these parasites could be classified both as endemic and threatened species, and the concept of co-threatened species should be applied to these parasites (Gómez & Nichols, 2013). Likely, there are additional trematode species in not yet studied endemic hosts that would fall into the same category.

The deposition of parasites into publicly accessible museum collections is critically important. This is especially true for the descriptions of new species (Krell, 2016). As discussed above, an illustration of such need is the situation with *P. lintoni* and *H. nimia*, (Valdivia *et al*., 2010; Oliva *et al*., 2015, 2018). Thus, the authors strongly encourage researchers to deposit their specimens, both types and vouchers, in public collections. In Chile, the museums Museo Nacional de Historia Natural and Museo de Zoología at Universidad de Concepción, have helminthological collections receiving and curating specimens.

Although there has been an increase in the number of publications on trematodes in Chile in the past decades, there is a clear need for training parasitologists who would apply modern integrative approaches, and more broadly use experimental models. There is an obvious need for geographic and taxonomic expansion of trematodological research in the country in order to investigate not yet studied regions and host species.

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On the taxonomy of Afrotropical Coleophoridae (V). New species of the genus *Coleophora* from Namibia (Lepidoptera, Coleophoridae)

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[2] *Contribution to the knowledge of Coleophoridae CXLVIII*

Abstract: This work presents a review of the Coleophoridae of Namibia. In addition to the list of 27 species known to date, 14 new species are described: *Coleophora magnaefontis* sp. nov., *C. gondwanae* sp. nov., *C. exotica* sp. nov., *C. pectinella* sp. nov., *C. abstrusa* sp. nov., *C. ausensis* sp. nov., *C. demiranda* sp. nov., *C. sandveldensis* sp. nov., *C. amaurosella* sp. nov., *C. omatakoella* sp. nov., *C. hobaterensis* sp. nov., *C. linteella* sp. nov., *C. leesi* sp. nov., *C. spatulifera* sp. nov.

Keywords: Lepidoptera - Coleophoridae - *Coleophora* - new species - Namibia - Afrotropical Region.

INTRODUCTION

Until the 21st century, no species of Coleophoridae was known for Namibia. Following recent researches and specimen collecting, especially by Wolfram Mey, many species have been discovered, most of them new to science (Baldizzone & van der Wolf, 2004, 2011, 2015). In addition to the new species described from material collected in Namibia, four other species records were added to the Namibian fauna. They had been described before this by E. Meyrick from South Africa: *C. scaleuta* Meyrick, 1911, *C. presbytica* Meyrick, 1911 (Meyrick, 1911; Baldizzone & van der Wolf, 2011), *C. textoria* Meyrick, 1921 (Meyrick, 1921; Baldizzone & van der Wolf, 2015), *C. oxyphaea* Meyrick, 1913 (Meyrick, 1913; Baldizzone, 2019b).
Until now, 27 species were known from Namibia, but many others will undoubtedly be added as new material is studied. The present work gives the descriptions of an additional 14 new species.

MATERIAL AND METHODS

Most of the Euparal slide mounts of dissected genitalia were photographed with a Bresser 5.0 camera attached to a Bresser BioScienze 40-1000x trinocular microscope, mainly using the Leitz PL Fluotar 6.3 / 0.20 objective. A few slides were photographed with an old Miranda camera body fitted with an adaptor tube to an old "Galileo" microscope equipped with Aus Jena 3:1-0.10 and 6.3:1-0.18 objectives. Black-and-white Ilford PAN F film was used to obtain images with high contrast between the structures and the background. Film negatives were digitized with a scanner then cleaned and edited in Corel PaintShop Pro. Adults were photographed with a Canon EOS 5D Mark II digital camera equipped with a Canon MP-E 65 mm objective, with lighting provided by two circular neon lamps OSRAM L 32W / 8400 C (cool white).
Morphological terms follow Baldizzone (2019a).

Abbreviations

Bldz = Giorgio Baldizzone, Asti, Italy
GP = genitalia preparation
MfN = Museum für Naturkunde, Berlin, Germany
NHMUK = Natural History Museum, London, U.K. (formerly British Museum of Natural History = BMNH)
RSA = Republic of South Africa
TMSA = Ditsong National Museum of Natural History, Pretoria, South Africa (formerly Transvaal Museum)
Wf = Hugo W. van der Wolf, Nuenen, The Netherlands.

TAXONOMY

Coleophora magnaefontis sp. nov.

Figs 1, 17-21

Holotype: ♂ (GP Bldz 15309); "Namibia | Grootfontein | m. 1300 | 6.IV.2009 | Legit G. Bassi"; "Collezione G. Bassi | 40398", [19°31'S, 18°08'E]; in coll. Baldizzone, Asti.

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Paratypes: 1 ♂ (GP Bldz 17243); same date and locality; "Collezione | G. Bassi | 40271"; in coll. Bassi. – 1 ♂ (GP BMNH 27348) "Pretoria, Transvaal, Janse | 12.3.[19]15"; in coll. NHMUK.

Diagnosis: Species of general appearance pale ochraceous. The male genitalia do not resemble those of any other known Afrotropical species and are characterized by the shape of the short and stocky tegumen with the pedunculus strongly dilated on the outside, the small cucullus, and the large sacculus.

Description: Wingspan 9 mm. Head whitish, frons suffused with ochre. Antenna ochre; scape ochre with a tuft of short scales. Labial palpus whitish on inner side, ochre on outer side; second segment ca. 0.5 time length of third. Proboscis short. Thorax white, suffused with ochre medially. Tegula white, ochre on outer side. Forewing ochre, slightly lined white along costa, on subcostal veins, lower edge of cell, and anal fold; fringes light ochre. Hindwing light grey, including fringes. Abdomen light ochre.
Abdominal structures (Fig. 21): Anterior lateral struts about 2.5 times as long as posteriors. Transverse strut with proximal edge thin and linear, distal edge thicker and slightly curved. Tergal disks (3rd tergite) length about twice their width, covered with about 30 small spines.
Male genitalia (Figs 17-20): Gnathos knob globular. Tegumen short and stout, constricted in middle; pedunculus short, strongly dilated. Transtilla slender, linear. Valvula with dorsal margin expanded, irregularly shaped, covered with few setae ventrally. Cucullus small, short, rounded at apex. Sacculus large, more sclerotized and slightly jagged on outer edge, with small triangular protuberance at dorsal angle. Phallotheca conical, slightly curved, more thickly sclerotized dorsally. Five spine-shaped cornuti of different lengths, fused together in the shape of a claw.
Female genitalia: Unknown.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Otjozondjupa), RSA (prov. Gauteng).

Etymology: From the Latin *magnus* [*-a, -um*] = great, and *fons* [*-fontis*] = source, because the name "Grootfontein", in Afrikaans, means "the great source".

Coleophora gondwanae sp. nov.
Figs 2, 22-24

Holotype: ♂ (GP Bldz 13537); "RSA | Richtersveld | Numees | Helskloof Gate | 9-12.X.2001 | leg. W. Mey | LF"; BIOTA | 160 W lamp | 200482001702681" [28°17.58'S, 16°57.228'E, 626 m]; in coll. MfN.

Paratype: 1 ♂ (GP Bldz 15019); "Namibia | Fishriver | Gondwana Canyon Lodge | 17.4.2008 | leg. W. Mey" [27° 40.412'S, 17°49.199'E, 757 m]; in coll. MfN.

Diagnosis: Species of light brownish grey habitus, with a small dot in the forewing cell. The male genitalia are characteristic because the valvula, cucullus and sacculus do not have separating margins, but are completely fused. The most similar African species is *C. frivolella* Baldizzone & van der Wolf, 2005, known only from Katanga (Democratic Republic of Congo). This species differs from *C. gondwanae* sp. nov. in habitus by its small size (8 mm) and creamy white forewing. The male genitalia show some obvious differences: the much longer transtilla, thinner, united medially, the smaller sacculus with a straight lateral margin, the very small and conical phallotheca, sclerotized only apically.

Description: Wingspan 10-13 mm. Head whitish. Antenna whitish grey; scape without erected scales. Labial palpus long, white on inner side, brown on outer side with protruding scales almost completely covering third segment, latter about half as long as second. Proboscis short, of normal shape. Thorax whitish grey. Tegula whitish grey, scattered with brown scales on outer side. Forewing whitish grey, thickly suffused with brown scales and with a small brown dot in the cell; fringes light ochre. Hindwing including fringes grey. Abdomen dirty whitish.
Abdominal structures (Fig. 24): Anterior lateral struts about 2.5 times as long as posteriors. Transverse strut with proximal edge thin and linear, with distal edge thicker and curved. Tergal disks (3rd tergite) about 5.5 times as long as wide, covered with about 50 spines.
Male genitalia (Figs 22, 23): Gnathos knob globular. Tegumen stout, constricted in middle; pedunculus short, dilated on outside. Transtilla large, triangular. Valvula not evident. Cucullus short, larger at base. Sacculus small, with straight ventral edge and small rounded protuberance at ventral angle. Phallotheca curved, sclerotized dorsally and dilated at rounded apex, without cornuti.
Female genitalia: Unknown.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Karas), RSA (prov. Northern Cape).

Etymology: The name derives from the name of the ancient supercontinent Gondwana.

Coleophora exotica sp. nov.
Figs 3-4, 25-31

Holotype: ♂ (GP Bldz 15015); "Namibia, Fishriver | Gondwana Canyon Lodge | 17.4.2008 | leg. W. Mey", [27°40.412'S, 17°49.199'E, 757 m]; in coll. MfN.

Paratypes: 3 ♂ (GP Bldz 15042); "RSA, Richtersveld | Koeroegapvlakte | 14-16.X.2001 LF | leg. W. Mey", [S 28°14.116' E 17°01.509', 664 m]; in coll. MfN. – 4 ♂ (GP Bldz 17156, 17158), 1 ♀ (GP Bldz 17157) "Namibia, Rosh Pinah, Namuskluft, | 7.3.2014, LF| leg. W. Mey", [27°51.986'S, 016°52.033'E, 685 m]; in coll. MfN and coll. Baldizzone.

Diagnosis: Species of greyish appearance. The habitus is similar to that of *C. kruegeri* Baldizzone & van der Wolf, 2004, but the genitalia do not resemble those of any other Afrotropical species. The male genitalia are similar to those of *C. maculata* Baldizzone, 2016, from Armenia, of which only the male is known, with ivory-coloured forewing and brown longitudinal streaks. The differences are mainly the shape of the shorter tegumen, in the ventral border of the sacculus engraved on the inner side and the protuberance in the dorsal angle longer and more curved. In the female of *C. exotica* the shape of the ductus bursae is characteristic, with the two parts of different width, of which the distal one with a sclerotized central line.

Description: Wingspan 14 mm. Head white. Antenna white; scape without erected scales. Labial palpus long, white on inner side, ochre suffused on outer side; the second segment covered with long scales projecting up to the apex of the third which is half the length of the second. Proboscis vestigial. Thorax and tegula white. Forewing whitish grey suffused of brown scales more concentrated in the costal half and at the apex; fringes light grey. Hindwing grey; fringes light grey. Abdomen whitish grey.

Abdominal structures (Figs 28, 31): Anterior lateral struts about 1.5 times as long as posteriors. Transverse strut curved on distal edge, with proximal edge sclerotized only in a small portion in the centre. Tergal disks (3rd tergite) about 4.5 times as long as wide, covered with about 30 conical spines.

Male genitalia (Figs 25-27): Gnathos knob globular. Tegumen long, restricted in middle; pedunculus short, dilated on outside. Transtilla ribbon-shaped, dilated at the apex. Valvula oblong, well sclerotized, covered with numerous setae with external edge curved and prominent. Cucullus short, ear shaped. Sacculus with inclined ventral edge and very sclerotized, dorsal angle with a robust triangular protuberance slightly overtaking the apex of the cucullus. Phallotheca conical, sclerotized only on lateral side. Not cornuti.

Female genitalia (Figs 29, 30): Papillae anales narrow and long. Apophyses posteriores about twice long as the anteriores. Sterigma trapezoidal, wider than long, proximal edge almost straight, distal edge curved, provided with long bristles, widely hollowed in the middle by the sinus vaginalis. Ostium bursae large, oval. Colliculum calyx-shaped, with outer edges thickened by more sclerotized bands, which merge into the short distal part of the ductus bursae. Ductus bursae: the distal part, about as long as the sterigma is thin, almost entirely crossed by a sclerotized medial line; the proximal part, slightly longer than the distal one, twice as wide, completely transparent. Corpus bursae in the form of an elongated sac with a small oval signum with a short spiny protuberance.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Karas), RSA (prov. Northern Cape).

Etymology: The name derives from the Latin *exoticus* [*-a, -um*] = exotic.

Coleophora pectinella sp. nov.

Figs 5, 32-37

Holotype: ♂ (GP Bldz 15019); "Namibia | 50 km N Okahandja | 12.2.2007, LF | leg. J. Deckert", [21°35.447'S, 16°56.174 E, 1349 m]; in coll. MfN.

Paratypes: 1 ♀ (GP Bldz 17164) "Namibia | 50 km N Okahandja | 8.4.2008, LF | leg. W. Mey"; "BIOTA observatory | Erichsfelde | Aut. Falle 1", [21°35.447'S, 16°56.174'E, 1349 m]; in coll. MfN. – 1 ♀ (GP Wf. 6439); [South Africa] "NYALAZI Forest, 25-28. III.1968 | Potgieter & Goode"; in coll. TMSA.

Diagnosis: In habitus and male genitalia *Coleophora pectinella* sp. nov. resembles *C. katangica* Baldizzone & van der Wolf, 2005, species from Democratic Republic of Congo, of which only the male is known. In the male genitalia of *C. katangica* the transtilla is smaller, little sclerotized. The valvula is more evident with an elongated ventral part, the cucullus is longer, much less inclined, the phallotheca is different, with two juxta rods, one of which ends at the apex with a triangular tooth, while in *C. pectinella* it ends with five robust thorns. The female of *C. pectinella* is unmistakable because the pointed shape of the papillae anales and for the large asymmetrical V-shaped sclerotized structure, which delimits the ostium bursae.

Description: Wingspan 10 mm. Head whitish. Antenna light ochre; scape without erected scales. Labial palpus whitish, slightly ochre suffused on outer side; second segment about 0.5 times the third. Proboscis short. Thorax and tegula whitish. Forewing completely light ivory; fringes light ochre. Hindwing and fringes light ochre. Abdomen light ochre.

Abdominal structures (Figs 33, 37): No posterior lateral struts, transverse strut thin, slightly curved. Tergal disks (3rd tergite) about 2.5 times longer than wide, covered with about 35 conical spines.

Male genitalia (Figs 32, 34): Gnathos knob oval. Tegumen long, slightly restricted in middle; pedunculus short, dilated on outside. Transtilla triangular at the

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Figs 1-8. Adults of *Coleophora* spp. (1) *C. magnaefontis* sp. nov., paratype ♂. (2) *C. gondwanae* sp. nov., holotype ♂. (3) *C. exotica* sp. nov., holotype ♂. (4) *C. exotica* head in lateral view. (5) *C. pectinella* sp. nov., holotype ♂. (6) *C. abstrusa* sp. nov., holotype ♂. (7) *C. ausensis* sp. nov., holotype ♂. (8) *C. demiranda*, sp. nov., holotype ♂.

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Figs 9-16. Adults of *Coleophora* spp. (9) *C. sandveldensis* sp. nov., paratype ♀. (10) *C. amaurosella* sp. nov., holotype ♂. (11) *C. omatakoella* sp. nov., holotype ♂ (dorsal view). (12) *C. omatakoella*, lateral view. (13) *C. hobaterensis* sp. nov., paratype ♂. (14) *C. linteella* sp. nov., holotype ♂. (15) *C. leesi* sp. nov., paratype ♂. (16) *C. spatulifera* sp. nov., paratype ♀.

apex, joined in middle. Valvula irregularly shaped, well sclerotized on the dorsal edge, narrow and elongated on the ventral edge. Cucullus robust, inclined, rounded at the apex. Sacculus narrow and long, very sclerotized on the ventral edge, with a long sharp tip in the ventral angle and a small tooth in the dorsal angle. Phallotheca tubular, sclerotized in the ventral part, with five long parallel spines of scalar length on one side at the apex. There are no cornuti.

Female genitalia (Figs 35, 36): Papillae anales well sclerotized, larger at the base, ending pointed at the apex. Apophyses posteriores robust, about twice as long as the anteriores. Sterigma trapezoidal, slightly longer than wide, with curved proximal edge, with sparse and thin bristles, hollowed in the middle by the short sinus vaginalis delimited by a large V-shaped sclerotized structure that opens at the distal edge of the sterigma. Ostium bursae small, oval. Colliculum large in the shape of an elongated amphora. Ductus bursae: the distal part is very short and tubular; the proximal part is long, transparent, finely dotted and widens proceeding towards the corpus bursae. The corpus bursae is shaped like a very elongated sac, without signum.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia [prov. Otjozondjupa], RSA (prov. KwaZulu-Natal).

Etymology: The name derives from the Latin *pecten* [*-inis*] = comb, in consequence of the shape of the spines on the apex of phallotheca.

Remarks: In the female genitalia of the Namibian specimen examined, a fragment of one of the spines located at the apex of the male phallotheca is evident above the sterigma.

Coleophora abstrusa sp. nov.

Figs 6, 38-42

Holotype: ♂ (GP Bldz 15033); "Namibia, Namib | Vogelfederberg | 28.1.2009, LF | leg. W. Mey", [23°03'S 14°59'E, 493 m]; in coll. MfN.

Paratypes: 2 ♂ (GP Bldz 16246) same collection data as holotype; in coll. MfN and Baldizzone.

Diagnosis: In habitus and male genitalia *Coleophora abstrusa* sp. nov. resembles *C. namibiae* Baldizzone & van der Wolf, 2004. The main differences are as follows: in the male genitalia of *C. abstrusa* the tegumen is more restricted medially, the cucullus is smaller and shorter, the sacculus is thicker in the dorsal half with a large internal jagged protuberance, the cornuti are larger, less numerous, gathered in a bunch and not in a row.

Description: Wingspan 12 mm. Head white, light brown suffused dorsally. Antenna whitish ochre; scape whit short tuft of scales. Labial palpus white, partially ochre suffused on outer side. Proboscis of normal shape. Thorax whitish. Tegula light brown. Forewing hazelnut colour, slightly clearer in the dorsal part; white line along the costa ending before the apex; fringes light ochre. Hindwing and fringes light grey.

Abdominal structures (Fig. 42): Anterior lateral struts about 3 times as long as posteriors. Transverse strut with proximal edge linear and ticker and distal edge, slightly curved in middle. Tergal disks (3rd tergite) about 5 times as long as wide, covered with about 30 spines.

Male genitalia (Figs 38-41): Gnathos knob globular. Tegumen stout, restricted in middle; pedunculus short, slightly dilated. Transtilla thin, linear, slightly dilated and oval at the apex. Valvula small, elongated, more sclerotized on the ventral edge. Cucullus very short, larger at the base. Sacculus with lateral edge very sclerotized, in the shape of an irregular triangle, with a small central tip; the inner edge is thicker and jagged in the dorsal half. Phallotheca conical, pointed at the apex, sclerotized only on the ventral and lateral sides. Cornuti about 20 in the shape of spines of different length, gathered at the base.

Female genitalia: Unknown.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Erongo).

Etymology: The name derives from the Latin *abstrusus* [*-a, -um*] = abstruse, complicated, due to the peculiar shape of the male genitalia.

Coleophora ausensis sp. nov.

Figs 7, 43-46

Holotype: ♂ (GP Bldz 16932); "S. W. AFRICA (11) | Aar Farm, 25 mls. ESE Aus | 15-17.i.1972"; "Southern African Exp | B. M. 1972-1";"NHMUK 010897636" [with QR code]; in coll. NHMUK.

Diagnosis: The species belongs to the group of *C. diffusa* Meyrick, 1913, to which there are also *C. kamiesella* Baldizzone & van der Wolf, 2015, *C. kuruensis*, Baldizzone, 2019, *C. rhabdophaeella* Baldizzone, 2019, *C. venusta* Baldizzone & van der Wolf, 2020b. The most similar species for the habitus and male genitalia is *C. venusta*. Compared to this species in the male genitalia of *C. ausensis* sp. nov. the transtilla is longer and thinner, with an angle at the base, the valvula is smaller and the protuberance on its external side is shorter, the cucullus is thinner, the horn-shaped protuberance in the dorsal angle is less sclerotized in the central part and its external base has a large triangular protuberance, the cornuti are much smaller and divided in two parts in a characteristic way.

Description: Wingspan 13 mm. Head white. Antenna white, ringed light ochre; scape white on outer side,

ochre on inner side, with short erected scales. Labial palpus white; the second article about 0.5 longer than the third. Proboscis short, of normal shape. Thorax and tegula whitish grey. Forewing brown, streaked white along the costa whit a line reaching the apex and irregularly in middle; costal fringes white, dorsal fringes light brown. Hindwing grey; fringes light ochre. Abdomen ochre.

Abdominal structures (Fig. 46): Anterior lateral struts about 0.5 times as long as posteriors. Transverse strut with proximal edge linear and not evident, distal edge curved in middle. Tergal disks (3rd tergite) about 3.5 times as long as wide, covered with about 50 spines.

Male genitalia (Figs 43-45): Gnathos knob oval. Tegumen long, slightly restricted in middle; pedunculus dilated externally. Transtilla angle shaped at the base, linear in distal part. Valvula small, oval, with outer edge rounded and prominent. Cucullus club-shaped, narrower at the base than at the apex. Sacculus rounded at the ventral edge, inclined on the lateral edge, ending with a robust and pointed horn-shaped protuberance as long as 2/3 of the cucullus; at its base the outer edge is expanded in the shape of a triangle rounded at the apex. Phallotheca long, conical, more sclerotized on 2/3 proximal part. Cornuti about 10 in the shape of spines of different length, gathered at the base; an isolated nail-shaped cornutus is located proximal to the others.

Female genitalia: Unknown.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Karas). South West Africa was the name for modern-day Namibia when it was under South African administration, from 1915 to 1990.

Etymology: The name derives from the locality where the specimen was collected.

Coleophora demiranda sp. nov.

Figs 8, 47-50

Holotype: ♂ (GP Bldz 15012); "Namibia, Fishriver | Gondwana Canyon Lodge | 17.4.2008 | leg. W. Mey", [07°40.412' S, 17°49.199'E, 757 m]; in coll. MfN.

Diagnosis: *Coleophora demiranda* sp. nov. is similar to *C. sclerisaccula* Baldizzone, 2019 for the structure of the male genitalia, while the habitus is different. In *C. sclerisaccula* the forewing is brown with line along the costa, while in *C. demiranda* the forewing is light ochre, with some white stripes. In the male genitalia, compared to *C. sclerisaccula* (Fig. 50) the most evident differences are: shorter transtilla, almost square and not oblong valvula, longer cucullus, more dorsally sclerotized phallotheca, cornuti of different shape arranged in an unordered way.

Description: Wingspan 17 mm. Head white. Antenna white; scape whit a tuft on long erected scales. Labial palpus short, white; the second segment twice the length of the third. Proboscis short, without circumvolution. Thorax and tegula white. Forewing light ochre, paler in proximal half and in the area between anal fold and costa, streaked with white lines: a large along the costa involving the fringes, a short curved on the lower edge of the cell, one along the anal fold, a large from the base along the dorsum; dorsal fringes light grey. Hindwing dark brown; fringes light grey. Abdomen white.

Abdominal structures (Fig. 48): Anterior lateral struts about 0.5 times as long as posteriors. Transverse strut tick and linear. Tergal disks (3rd tergite) length about twice their width, covered with about 50 spines.

Male genitalia (Figs 47, 49): Gnathos knob globular. Tegumen stout, slightly restricted in middle; pedunculus short, dilated externally. Transtilla, short, curved, nail shaped. Valvula big, rectangular, the lateral edge straight and more sclerotized. Cucullus long, club shaped, slightly restricted in middle. Sacculus narrow and curved, very sclerotized border in distal 2/3; dorsal angle with a small tooth. Phallotheca conical, curved, more sclerotized dorsally. Cornuti: 10 in the shape of pine needles of different length in the distal part and 4 in the shape of small spines united in a formation similar to a claw.

Female genitalia: Unknown.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Karas).

Etymology: The name derives from the Latin *demirandus* [*-a, -um*] = admirable, because of the nice habitus.

Coleophora sandveldensis sp. nov.

Figs 9, 51-57

Holotype: ♂ (GP Bldz 17159); "Namibia, Gamsb. | Rooiklip Farm, | 10.-11.3.2014 | leg. W. Mey", [23°24.382'S, 016°03.614'E, 1075 m]; in coll. MfN.

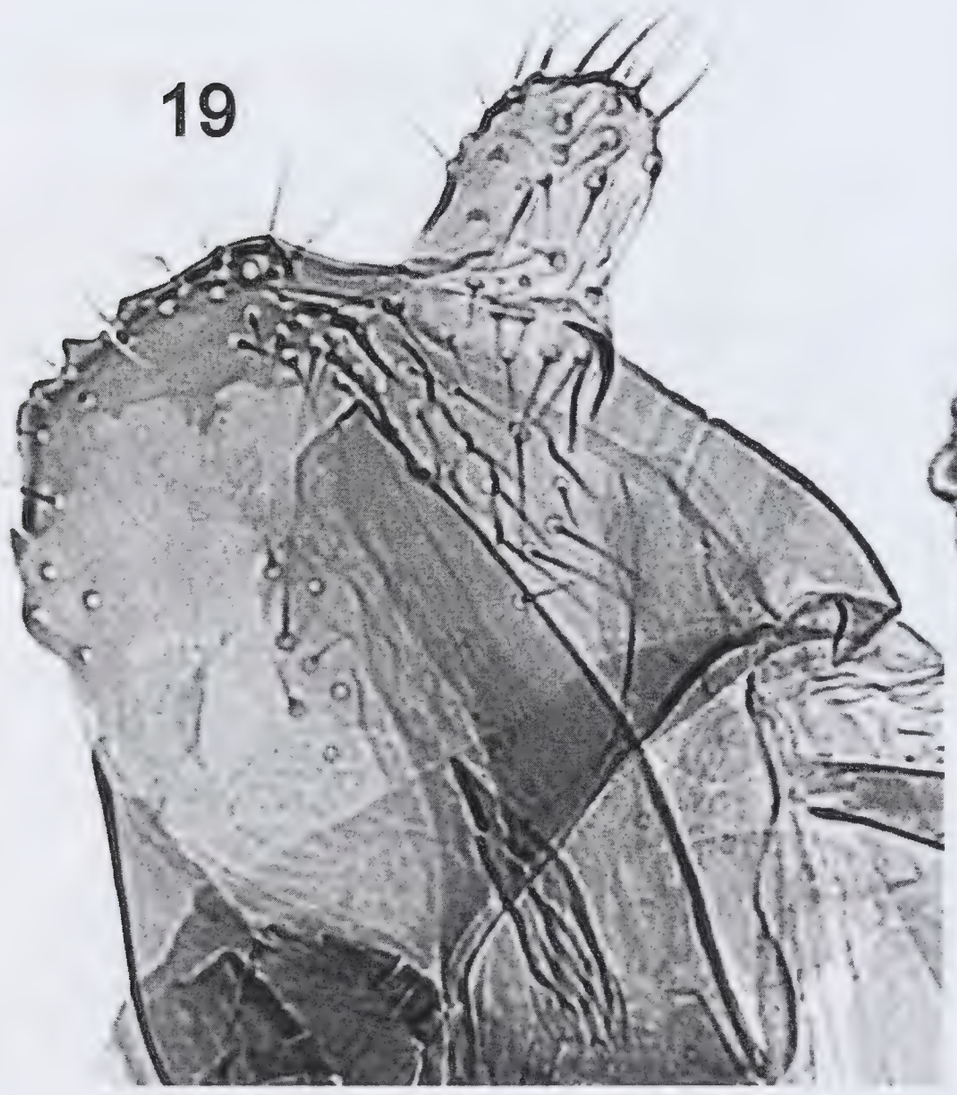
Paratypes: 2 ♀ (GP Bldz 15045, 17060); "Namibia, Sandveld | 60 km N Gobabis | 22.-26.1.2006, LF | leg. W. Mey", [22°04.33'S, 19°13.39'E]. In coll. MfN and coll. Baldizzone.

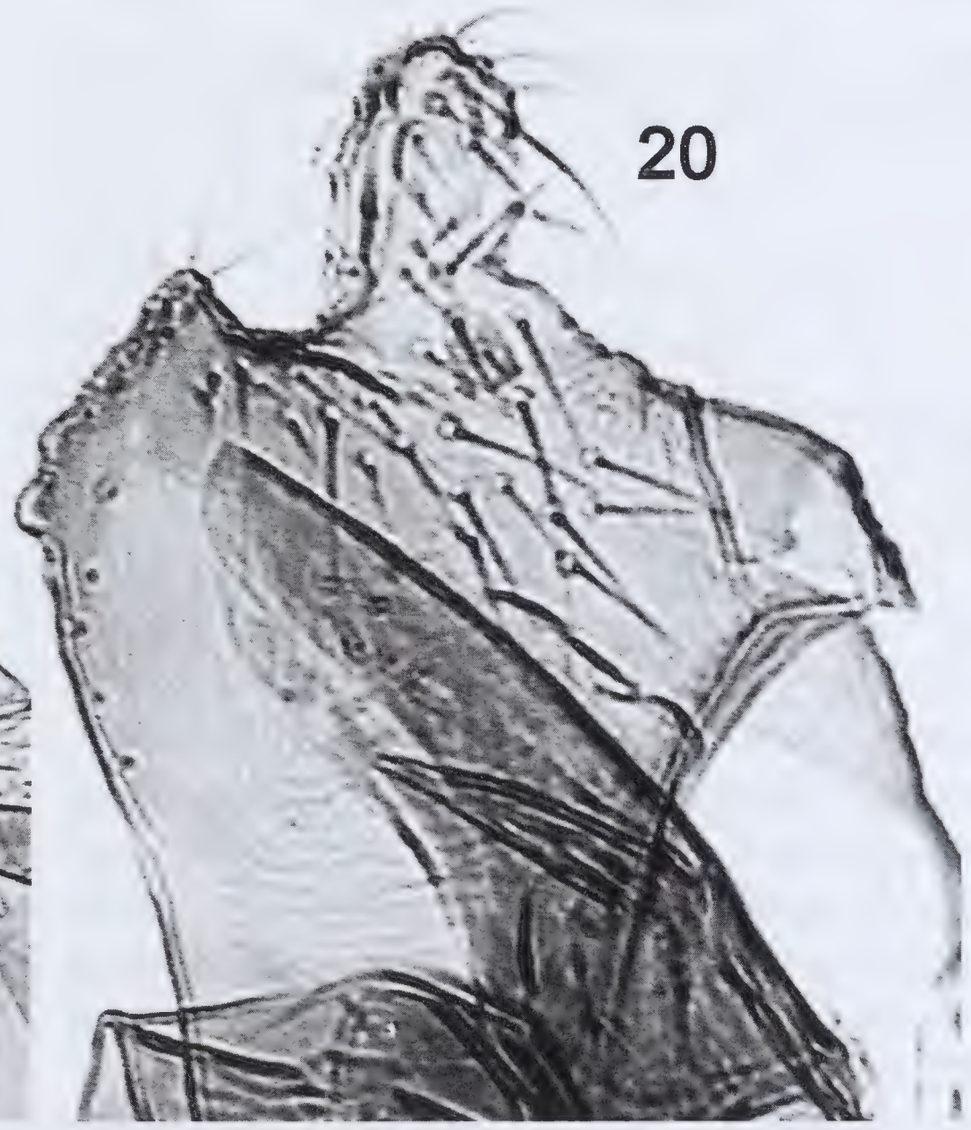
Diagnosis: Species with white forewing and elongated median triangular band of light hazelnut colour. The male genitalia does not resemble any other Afrotropical species and its shape resembles that of numerous Palearctic species, which have the forewing with silver streaks. The female genitalia resembles that of some Afrotropical species which have brown forewing with a white costal streak. It differs from all of them for the characteristic shape of the low and wide sterigma, hollowed out on the distal edge on both sides of the sinus vaginalis and for the large signum.

Description: Wingspan 12-13 mm. Head white. Antenna white; scape white, with a thick tuft of erected scales, tinged with ochre at apex; the second article is about twice as long as the third. Proboscis short. Thorax and tegula white. Forewing glossy white, light hazelnut coloured between the broad costal streak and the anal fold; costal fringes white, dorsal fringes light grey. Hindwing and fringes light grey. Abdomen white.

Abdominal structures (Fig. 54): No posterior lateral struts, transverse strut thin, slightly curved. Tergal disks (3rd tergite) about two times longer than wide, covered with about 60 conical spines.

Male genitalia (Figs 51-53): Gnathos knob globular. Tegumen stout, slightly restricted in middle; pedunculus short and large. Transtilla short and robust, inclined, rounded at the apex. Valvula large with slightly evident

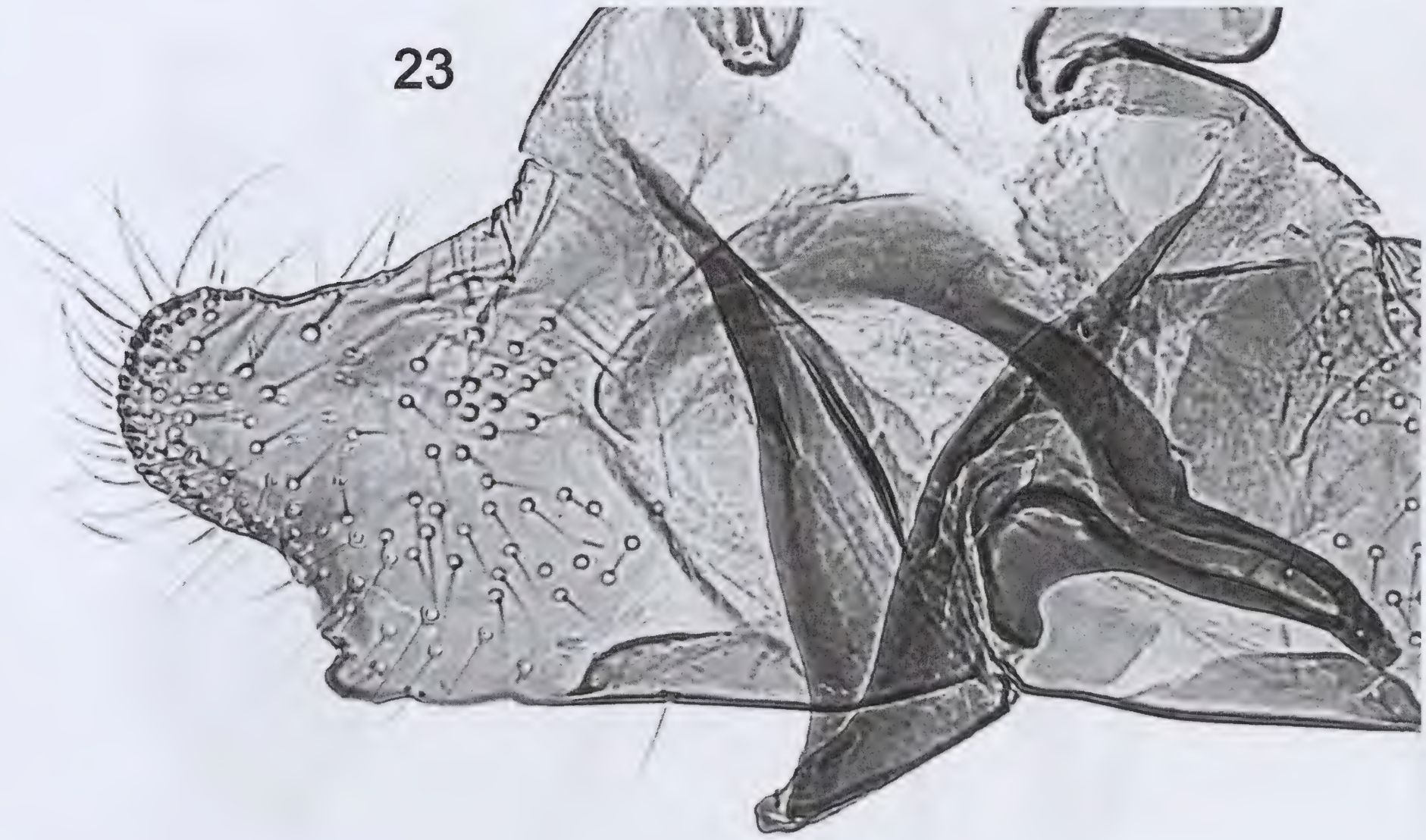




Figs 17-21. Male genitalia of *C. magnaefontis* sp. nov. (17) GP Bldz 15039, holotype. (18) Enlarged detail of cornuti. (19) Enlarged detail of valva, phallotheca and cornuti. (20) GP BMNH 27348, paratype, same detail. (21) Abdominal segments 1-5.

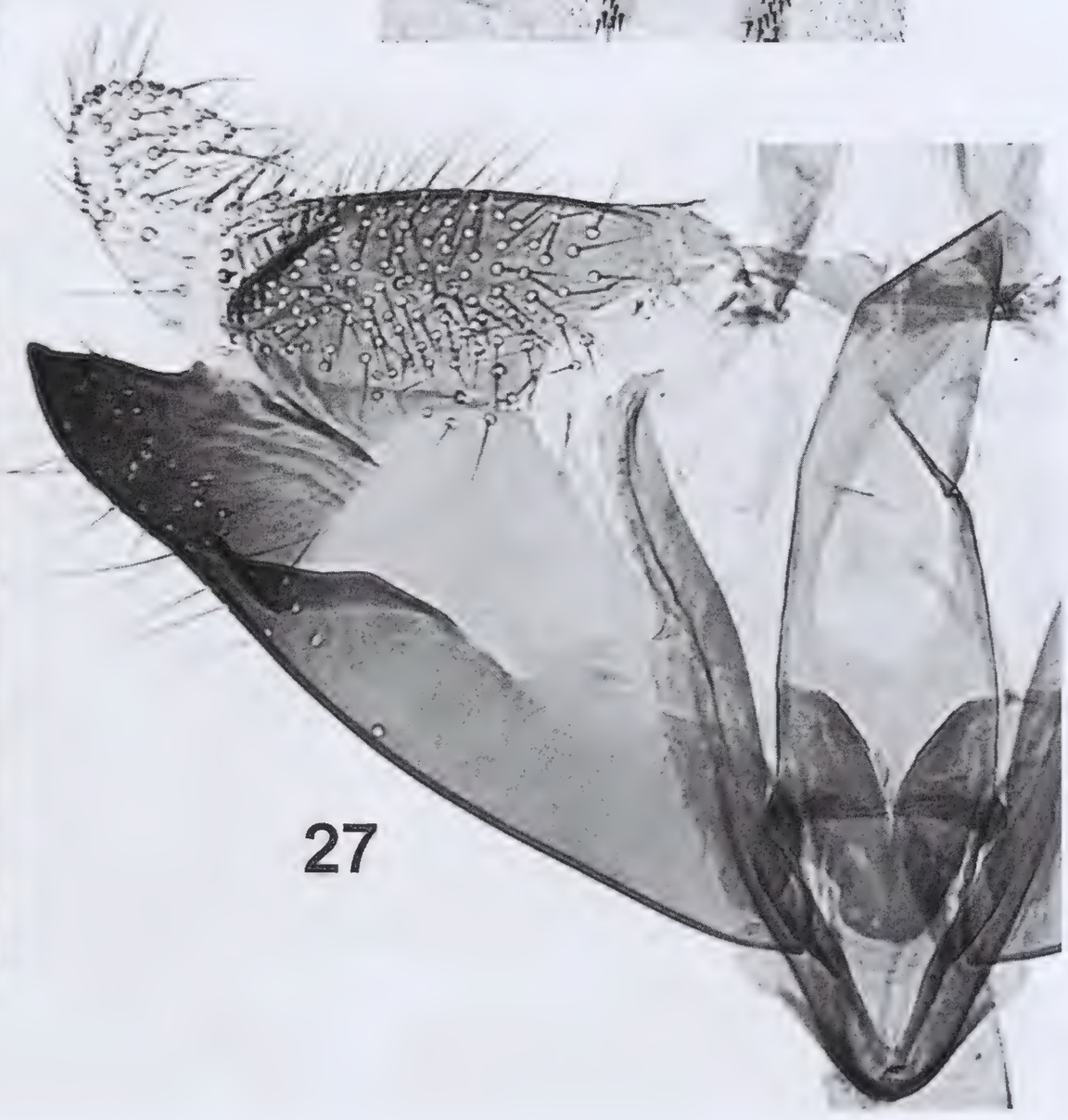
edges, except that on the outer side more sclerotized. Cucullus short, wider at the base. Sacculus curved on the ventral side with thickened edges, ending in the dorsal corner in triangular shape. Phallotheca large, conical, slightly more dorsally sclerotized. Cornuti very numerous in the form of spines of different lengths, shorter at the base and longer at the apex, gathered in a long claw-like structure.

Female genitalia (Figs 55-57): Papillae anales oval. Apophyses posteriores twice as long as the anteriores. Sterigma trapezoidal, about three times as wide as its height, distal edge hollowed out at the sides of the



Figs 22-24. Male genitalia of *C. gondwanae* sp. nov. (22) GP Bldz 15019, paratype. (23) GP 13537, holotype, enlarged detail of valva and phallotheca. (24) GP Bldz 15019, paratype, abdominal segments 1-4.

central part; sinus vaginalis broad, with 5-6 strong, short and sharp spines on either side of the distal edge. Ostium bursae broad, oval. Colliculum funnel-shaped, crossed by the end of the medial line. Ductus bursae: the distal part is long and thin, wrapped in small spines on two bands parallel to the medial line, which begins in the central convolution shortly after the insertion of the ductus seminalis; the proximal part of the ductus is wide and transparent in the convolution, then more sclerotized in small successive convolutions and thinner and more linear up to the bursa copulatrix shaped like an oval sac, with a large anchor-shaped signum, asymmetric in the laminar part.



Figs 25-28. Male genitalia of *C. exotica* sp. nov. (25) GP Bldz 15015, holotype. (26) Enlarged detail of valva. (27) GP Bldz 15042, paratype, enlarged detail of valva and phallotheca. (28) GP Bldz 15178, paratype, abdominal segments 1-5.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Windhoek, Khomas).

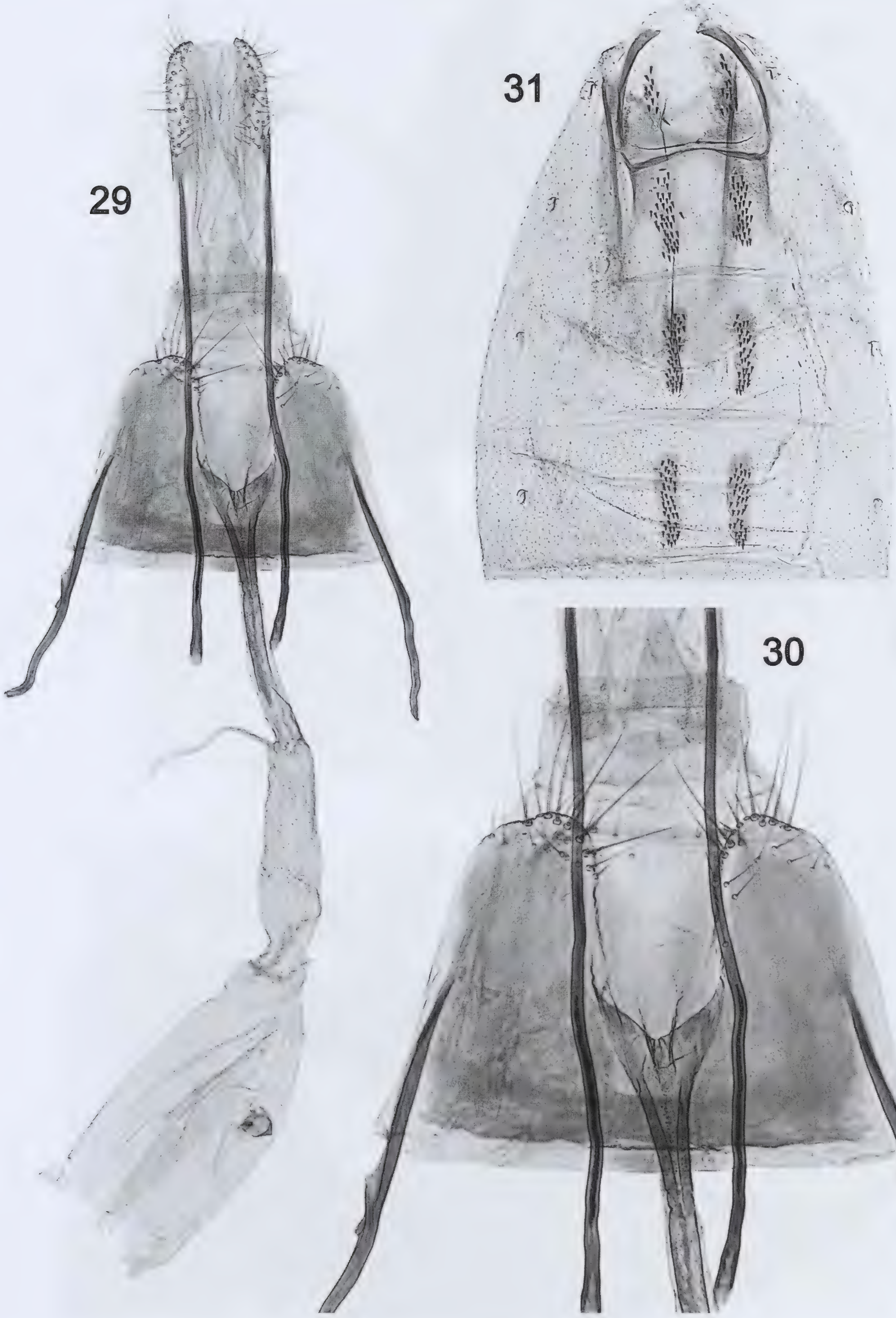
Etymology: The name derives from the locality where two specimens were collected.

***Coleophora amaurosella* sp. nov.**

Figs 10, 58-61

Holotype: ♂ (GP Bldz 13528); "Namibia, Omatako Ranch, LF | 22-23.III.2003 | leg. W. Mey", [21°30.429'S, 16°43.566'E, 1519 m]; in coll. MfN.

Diagnosis: *Coleophora amaurosella* sp. nov. does not resemble any other afrotropical species, but for the

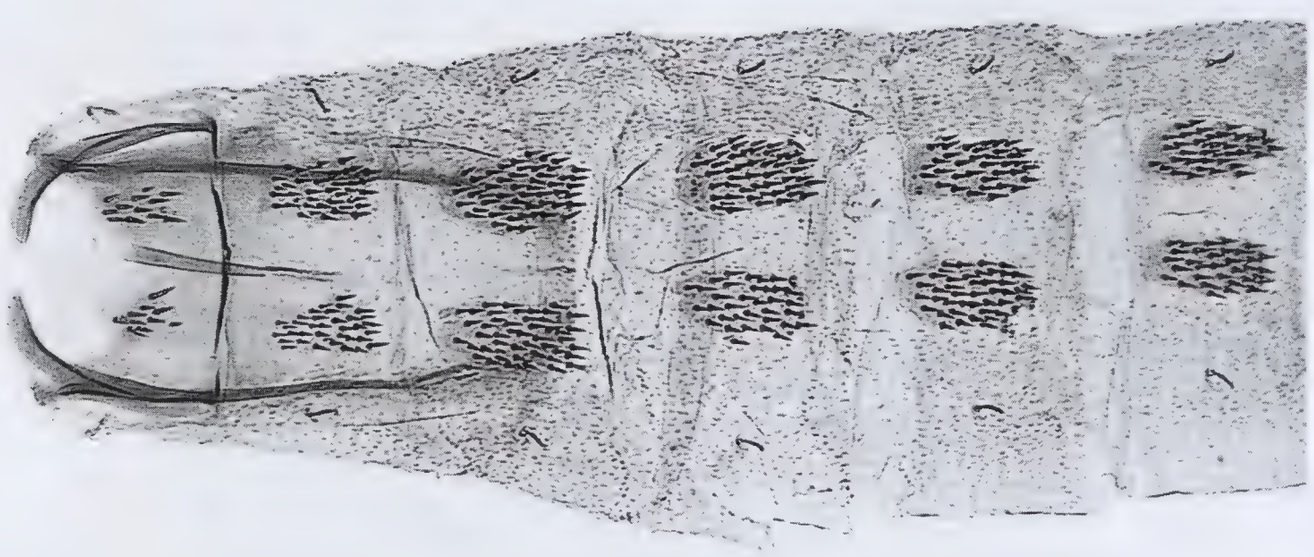


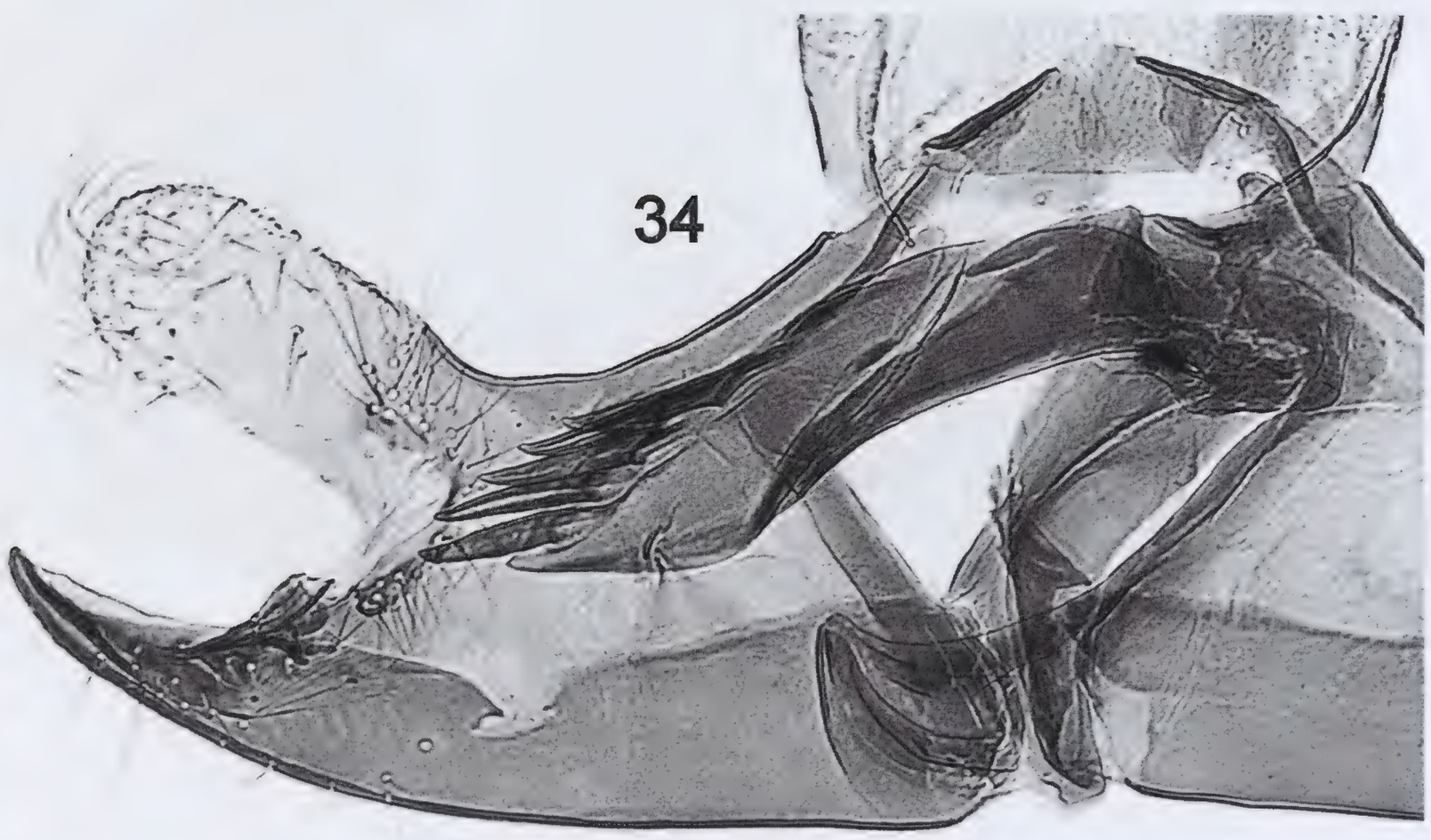
Figs 29-31. Female genitalia of *C. exotica* sp. nov. (29) GP Bldz 17157, paratype. (30) Enlarged detail of sterigma. (31) Abdominal segments 1-4.

male genitalia it is similar to Palearctic species of the *C. discordella* Zeller, 1849 group. From these species it differs in the shape of the sacculus, the conical phallotheca and the numerous short cornuti spiniform arranged irregularly.

Description: Wingspan 11 mm. Head white. Antenna ringed light ochre and whitish; scape without erected scales. Labial palpus white, slightly ochre suffused on the outer side; the second article about long as the third. Proboscis of normal shape. Thorax and tegula white. Forewing greyish ochre, lighter in the dorsal half and darker on the apex, streaked with slender whitish lines along the costa, in middle, along the anal fold and along the dorsum; fringes ochre. Hindwing grey; fringes light grey. Abdomen ochre.

Abdominal structures (Fig. 61): No posterior lateral struts. Transverse strut curved, with proximal edge thinner and



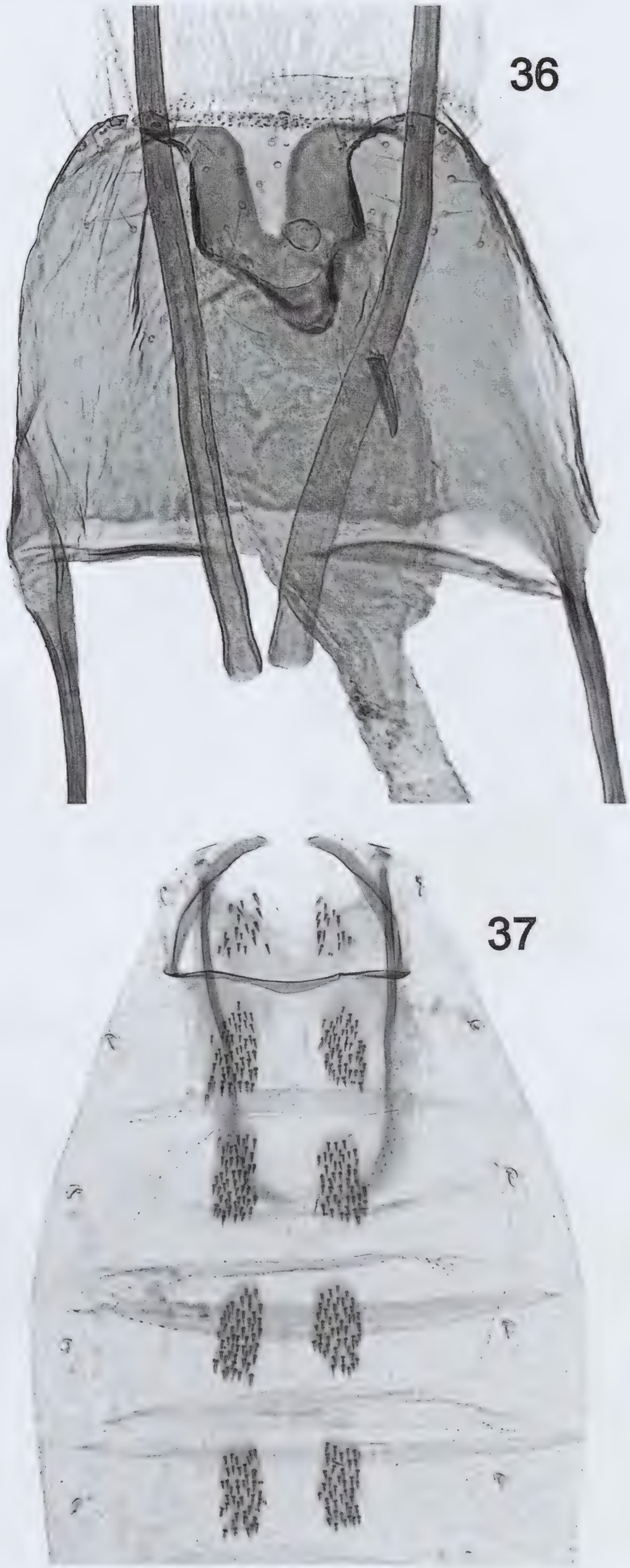


Figs 32-34. Male genitalia of *C. pectinella* sp. nov. (32) GP Bldz 15063, holotype. (33) Abdominal segments 1-6. (34) Enlarged detail of valve and phallotheca.

distal edge thicker, slightly narrowed in middle. Tergal disks (3rd tergite) about 3 times as long as wide, covered with about 50 spines.

Male genitalia (Figs 58-60): Gnathos knob globular. Tegumen stout, restricted in middle; pedunculus large. Transtilla short, triangular. Valvula suboval, covered by numerous short setae. Cucullus long, large at the base, restricted in middle, expanded and rounded at the apex. Sacculus with a long slender protuberance horn shaped in dorsal angle. Phallotheca short, conical, few sclerotized. Cornuti numerous, in the shape of small spines, gathered in a curved, irregular formation.

Female genitalia: Unknown.



Figs 35-37. Female genitalia of *C. pectinella* sp. nov. (35) GP Bldz 17164, paratype. (36) Enlarged detail of sterigma. (37) Abdominal segments 1-5.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Otjozondjupa).

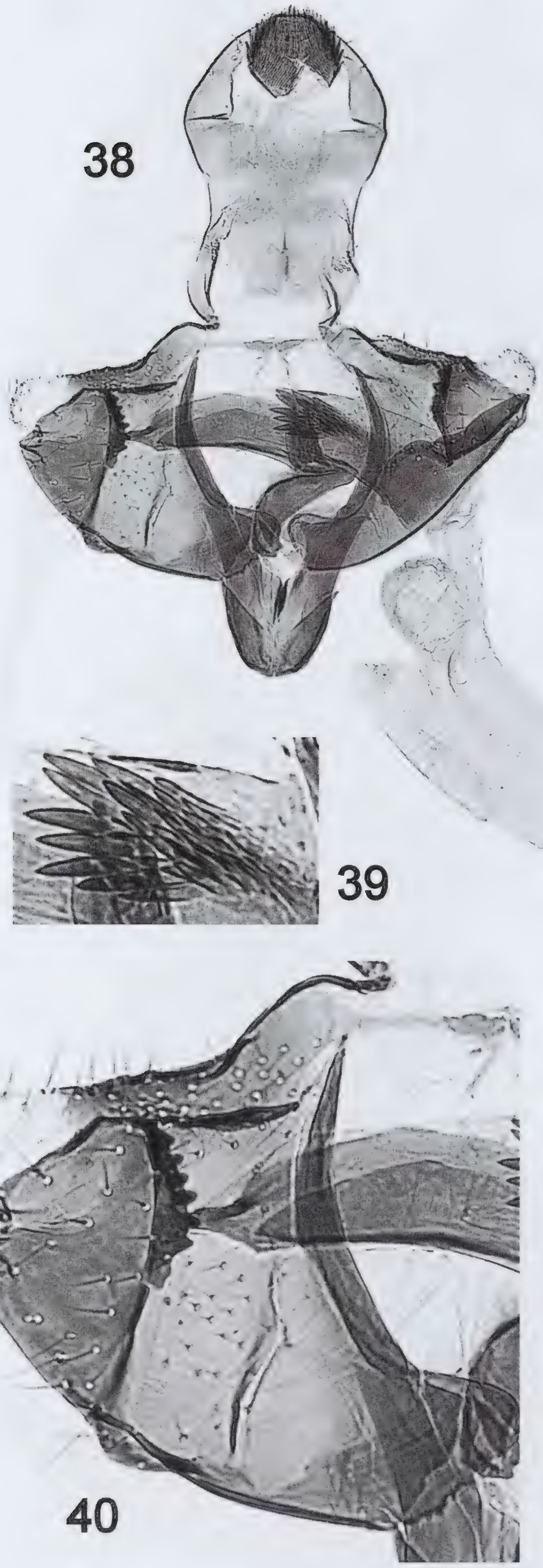
Etymology: The name derives from the Greek ἀμαυρός [- ά, -όν] = faded, due to the species habitus.

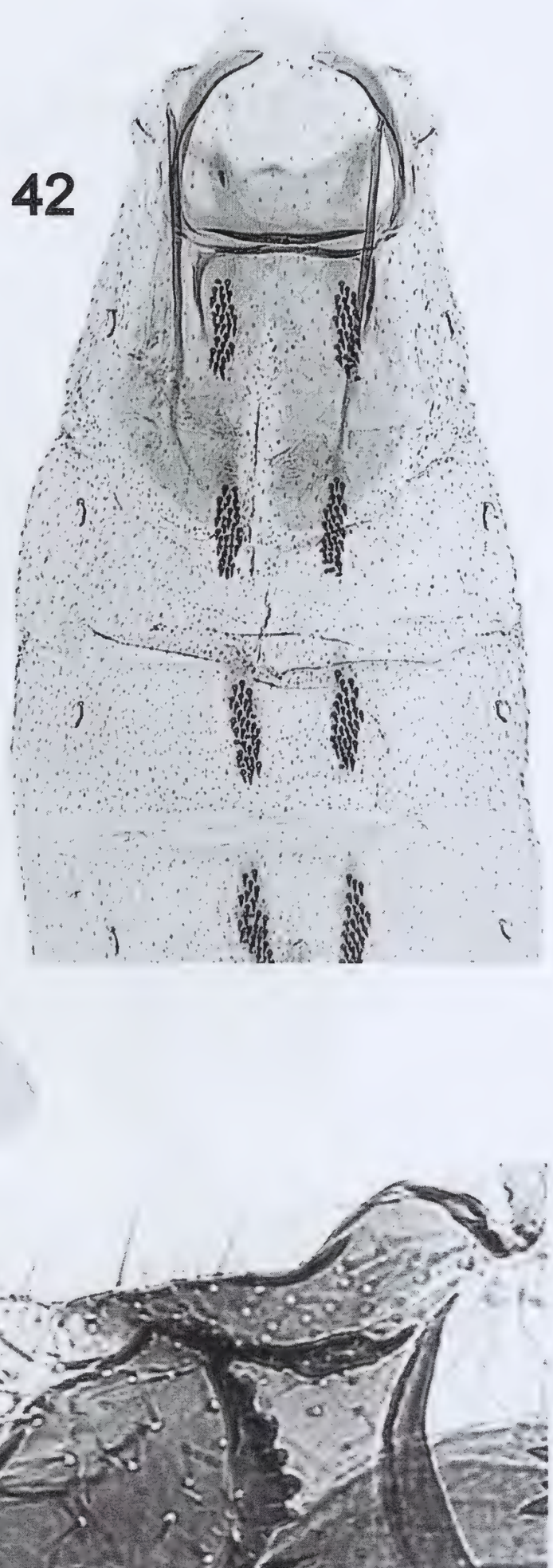
***Coleophora omatakoella* sp. nov.**

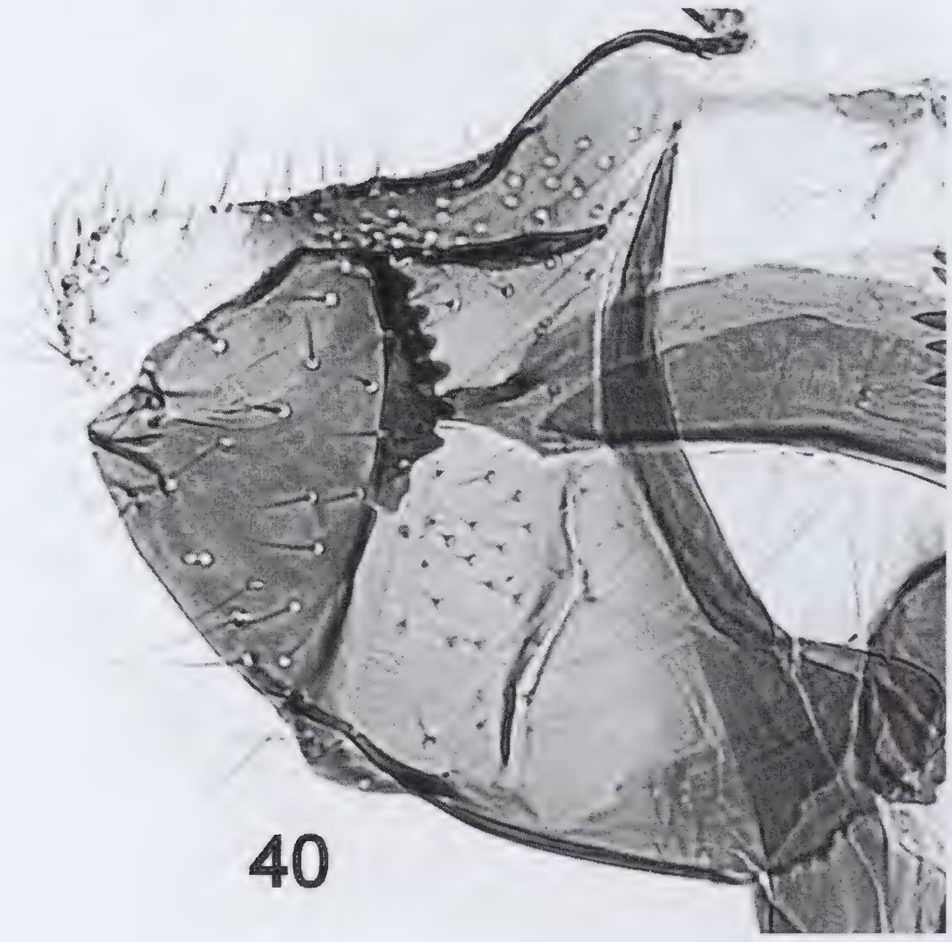
Figs 11-12, 62-65

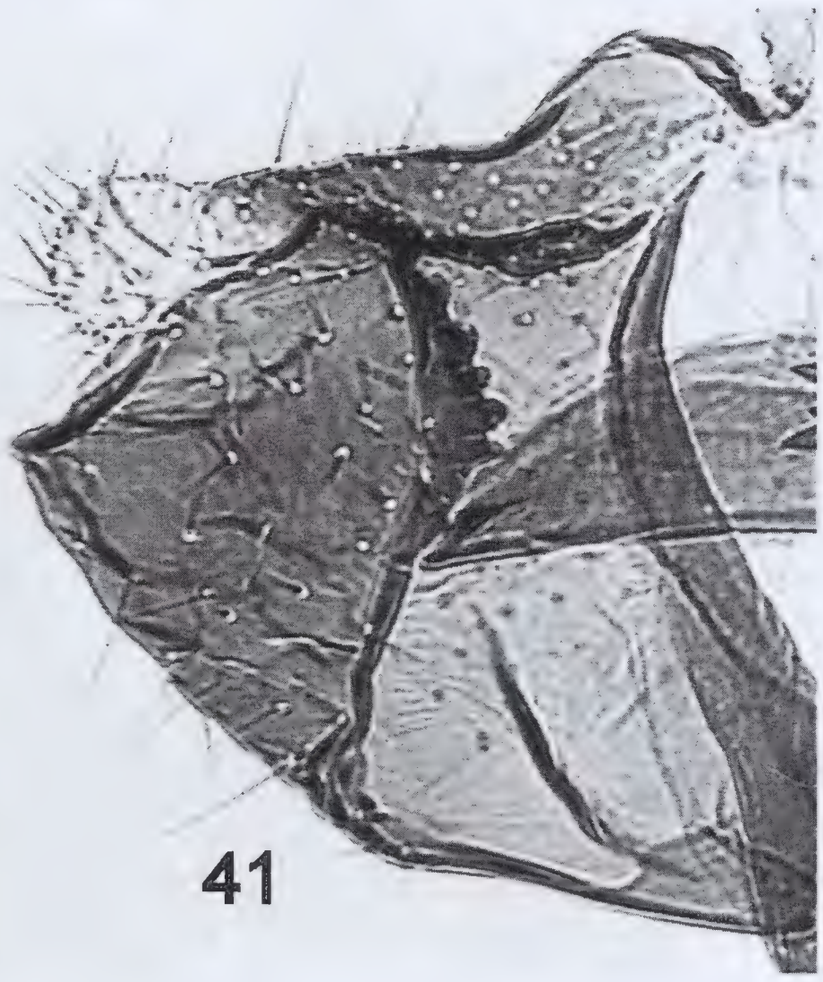
Holotype: ♂ (GP Bldz 13526); "Namibia, Omatako Ranch, LF | 22-23.III.2003 | leg. W. Mey", [1°30.429'S, 16°43.566'E, 1519 m]; in coll. MfN.

Diagnosis: Species with brown forewing, light shaded and streaked with some fine white lines. It does not resemble any species already known for the







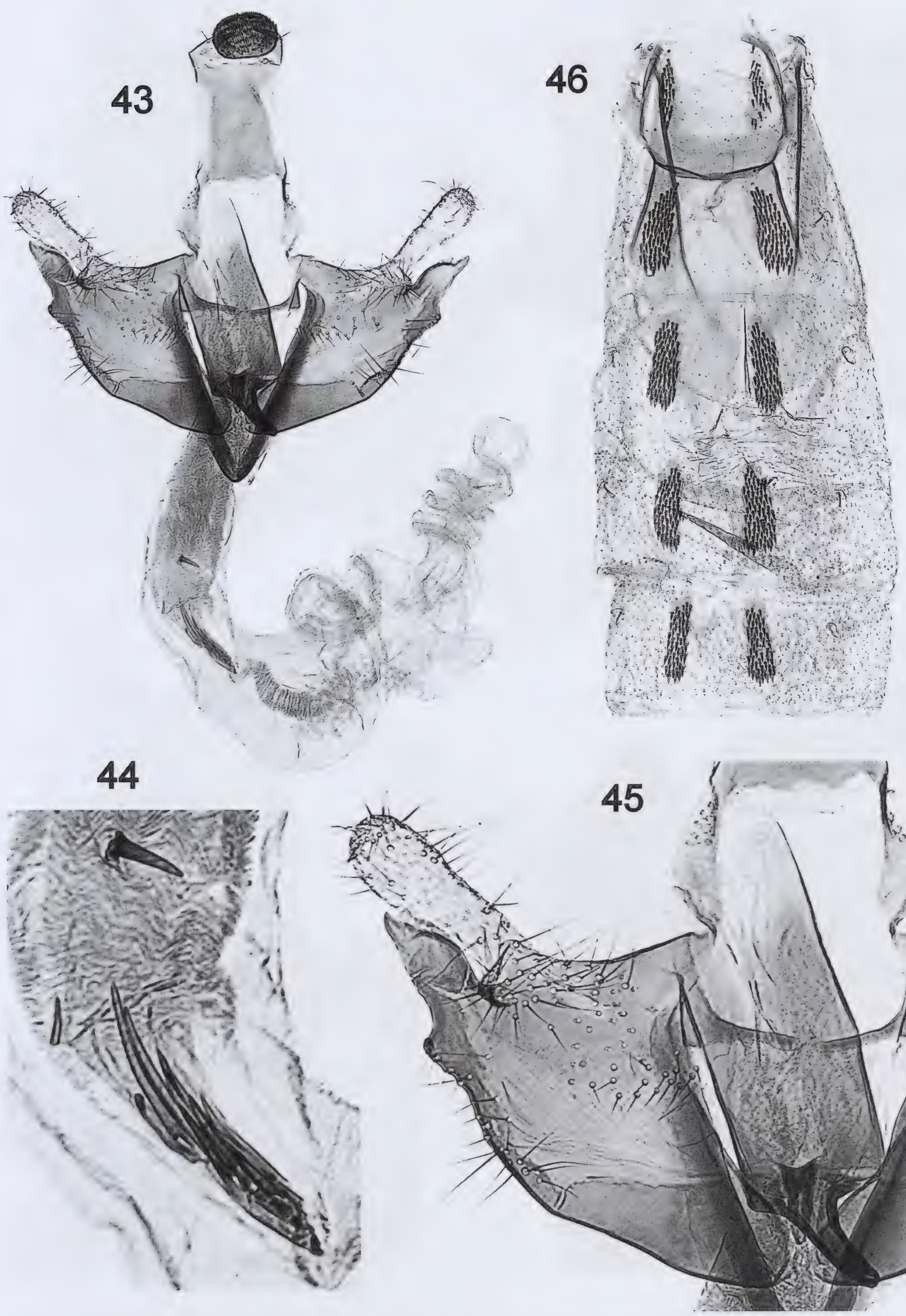


Figs 38-42. Male genitalia of *C. abstrusa* sp. nov. (38) GP Bldz 16246, paratype. (39) Enlarged detail of cornuti. (40) Enlarged detail of valva and phallotheca. (41) GP 15033, holotype, same detail. (42) Abdominal segments 1-5.

characteristic shape of the male genitalia, in particular for the outer edge of the sacculus and the curved vesica with a long row of cornuti extended for almost its entire length.

Description: Wingspan 14 mm. Head white. Antenna white; scape whit a tuft of erected scales, ochre on the inner side, white on the outer one. Labial palpus white on the inner side, ochre on the outer side; the second segment about 0.5 times longer than the third. Proboscis of normal shape. Thorax and tegula white. Forewing brown, lighter in the part between anal fold and costa, streaked with white lines: along the costa involving the first 1/3 of the fringes, along the anal fold, along the dorsum; fringes brown. Hindwing grey; fringes brown. Abdomen brown.

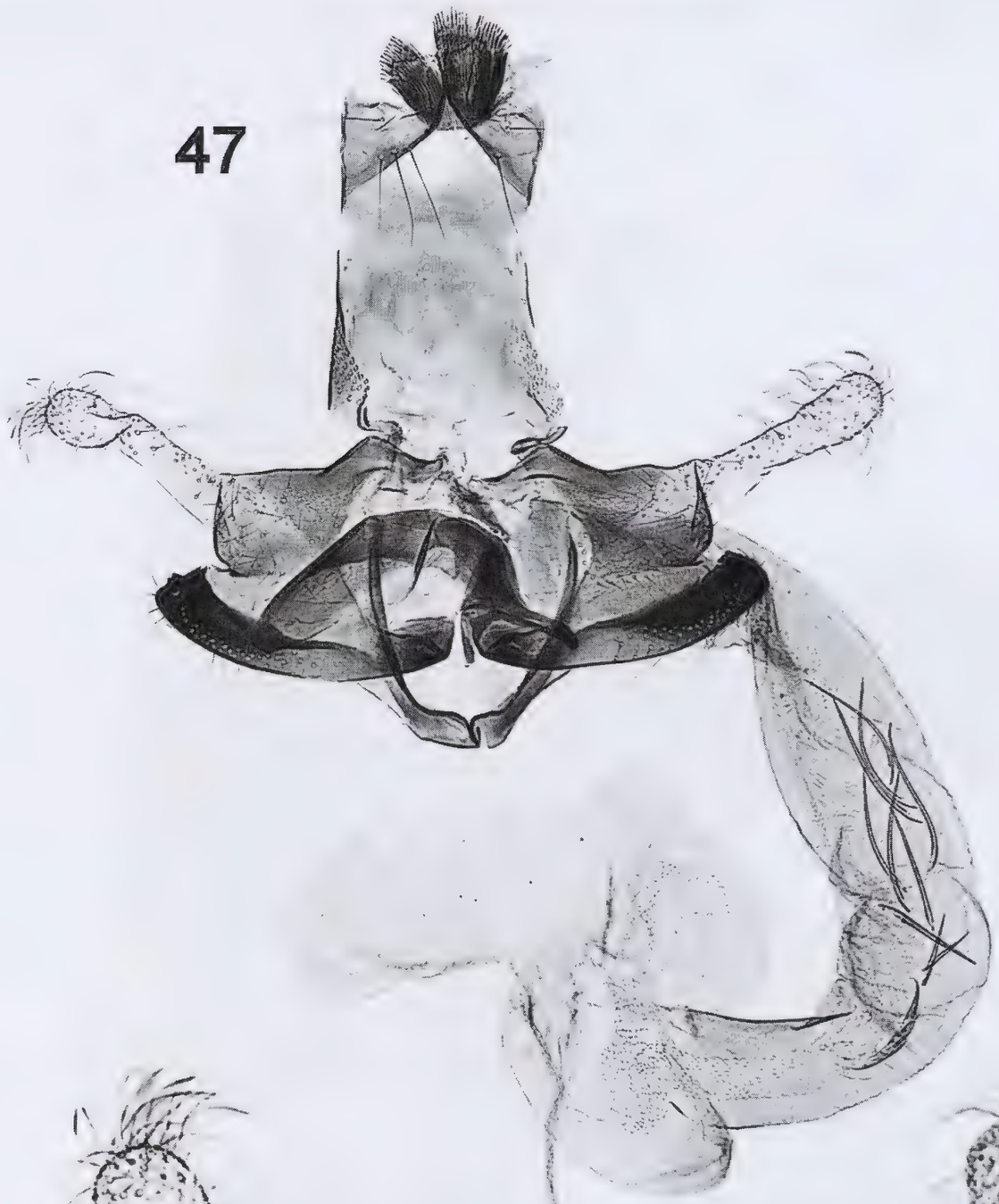
Abdominal structures (Fig. 65): Anterior lateral struts

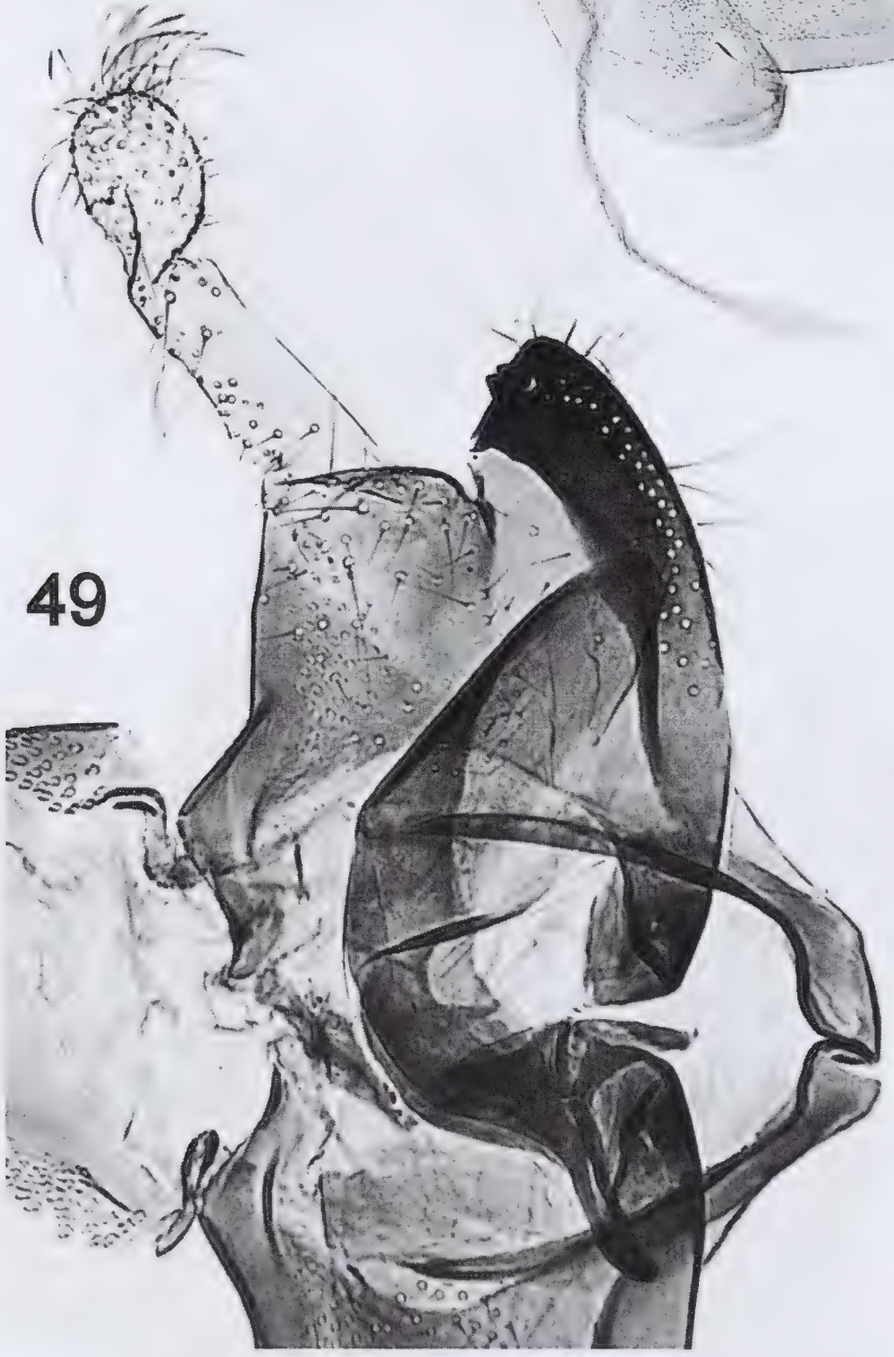


Figs 43-46. Male genitalia of *C. ausensis* sp. nov. (43) GP Bldz 16392, holotype. (44) Enlarged detail of cornuti. (45) Enlarged detail of valva and phallotheca. (46) Abdominal segments 1-5.

about 0.5 times as long as posteriors. Transverse strut linear with distal edge restricted in middle. Tergal disks (3rd tergite) about 4 times as long as wide, covered with about 50 spines.

Male genitalia (Figs 62-64): Gnathos knob globular. Tegumen stout, restricted in middle; pedunculus short and large. Transtilla long, slightly curved. Valvula large, whit lateral edge curved. Cucullus narrow slightly more expanded than the lateral edge of the sacculus. Sacculus expanded and more sclerotized on lateral edge, with a robust pointed protuberance and a little triangular protuberance at the dorsal angle. Phallotheca long,





Figs 47-50. Male genitalia of *C. demiranda* sp. nov. (47) GP Bldz 15012, holotype. (48) Abdominal segments 1-5. (49) Enlarged detail of valva and phallotheca. (50) Male genitalia of *C. sclerisaccula* Baldizzone, 2019, enlarged detail of valva and phallotheca.

conical, sclerotized on the lateral sides. Cornuti very numerous in the shape of spines of different length, gathered in a formation as long almost as the whole vesica.
Female genitalia: Unknown.

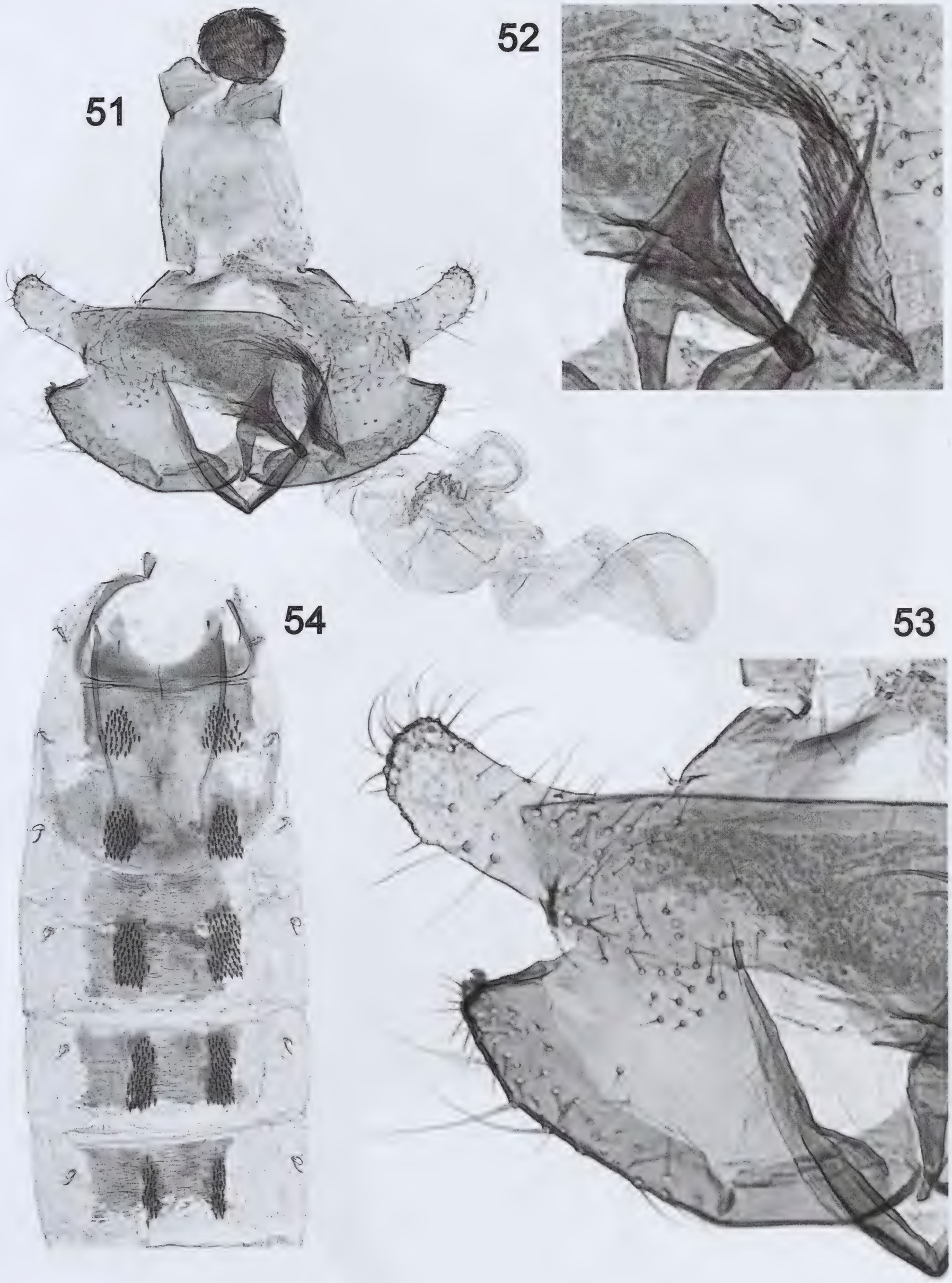
Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Otjozondjupa).

Etymology: The name derives from the locality where the specimen was collected.

***Coleophora hobaterensis* sp. nov.**
Figs 13, 66-69

Holotype: ♂ (GP Bldz 14981); "Namibia, Hobatere Lodge, campsite | 19.- 21.II.2008, LF | leg. W. Mey" [19°19.016'S, 14°28.153'E, 1256 m]; in coll. MfN.

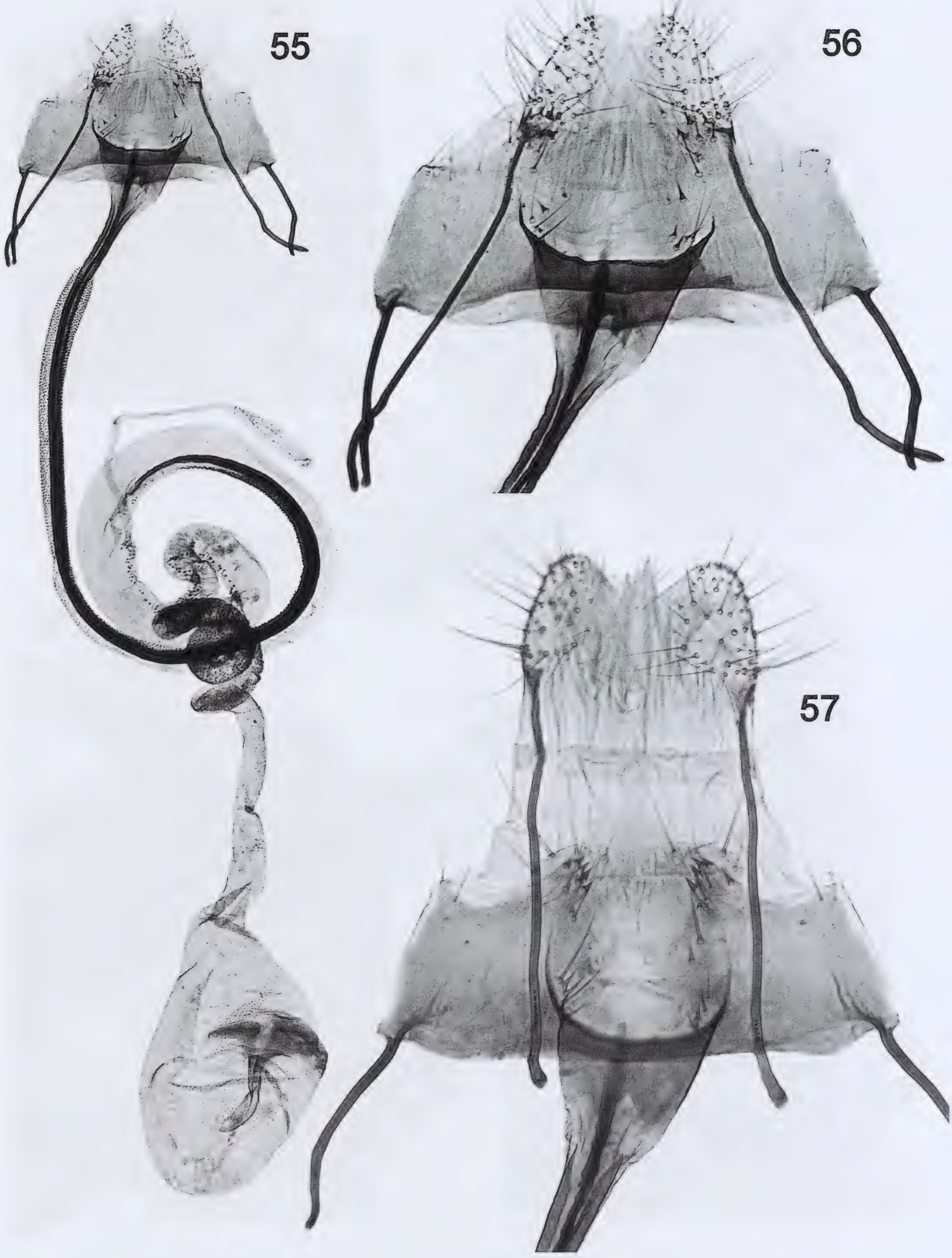


Figs 51-54. Male genitalia of *C. sandveldensis* sp. nov. (51) GP Bldz 17159, holotype. (52) Enlarged detail of cornuti. (53) Enlarged detail of valva and phallotheca. (54) Abdominal segments 1-6.

Paratypes: 5 ♂ (GP Bldz 14984, 14985, 15052); same collection data as holotype; in coll. MfN and coll. Baldizzone.

Diagnosis: Species of light brown appearance, with brownish forewings finely white streaked. The male genitalia does not resemble that of any other known Afrotropical species. The main peculiarities consist in the shape of the sacculus and in that of the phallotheca.

Description: Wingspan 10-11 mm. Head light brown, white upper the eye. Antenna brown; scape whitish without erected scales. Labial palpus brown lighter on the inner side; the second article about as long as the

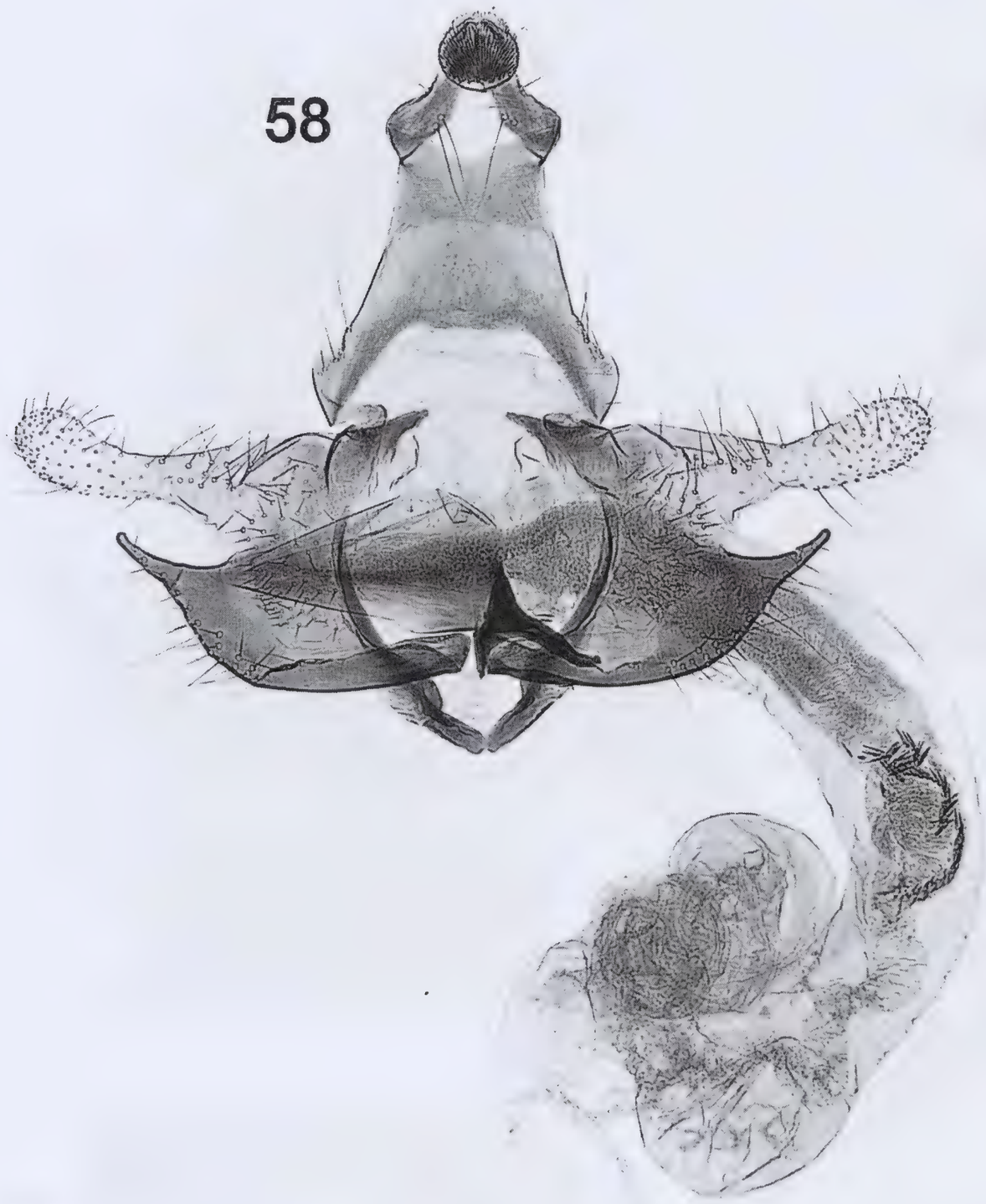


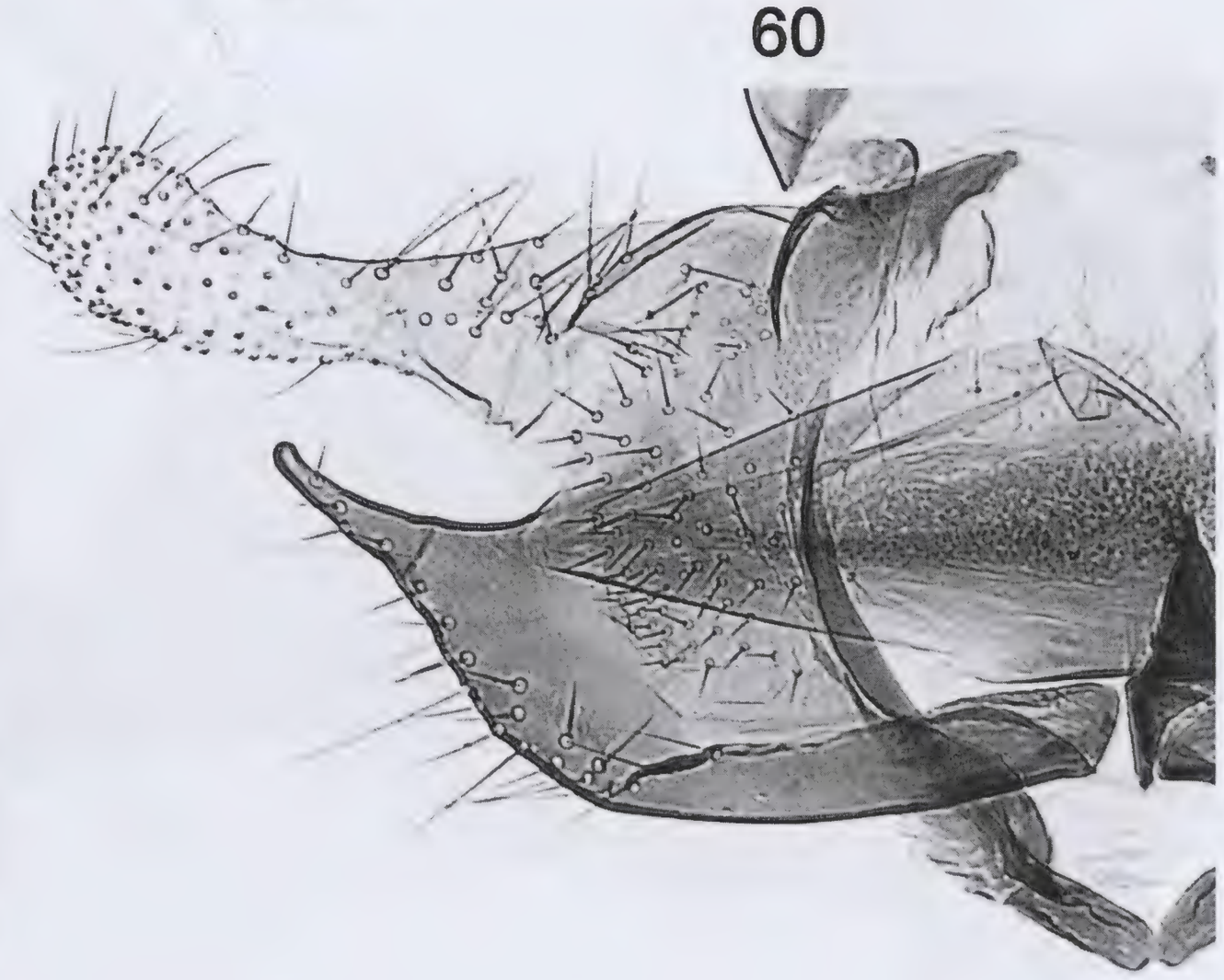
Figs 55-57. Female genitalia of *C. sandveldensis* sp. nov. (55) GP Bldz 15045, paratype. (56) Enlarged detail of sterigma. (57) GP Bldz 17160, same detail.

third. Proboscis of normal shape. Thorax and tegula brownish. Forewing brownish, finely streaked with slender whitish lines along the costa and the veins; fringes light ochre. Hindwing grey; fringes light ochre. Abdomen ochre.

Abdominal structures (Fig. 69): No posterior lateral struts. Transverse strut thin, with proximal edge slightly curve and distal edge straight, thinner in middle. Tergal disks (3rd tergite) about 3.5 times as long as wide, covered with about 35 spines.

Male genitalia (Figs 66-68): Gnathos knob globular. Tegumen quite narrow in middle; pedunculus expanded externally. Transtilla narrow joined in middle. Valvula small, irregularly oval, covered by many setae. Cucullus short, stout, large at the base, ear-shaped. Sacculus short, with a little rounded protuberance on the ventral





Figs 58-61. Male genitalia of *C. amaurosella* sp. nov. (58) GP Bldz 13528, holotype. (59) Enlarged detail of cornuti. (60) enlarged detail of valva and phallotheca. (61) Abdominal segments 1-5.

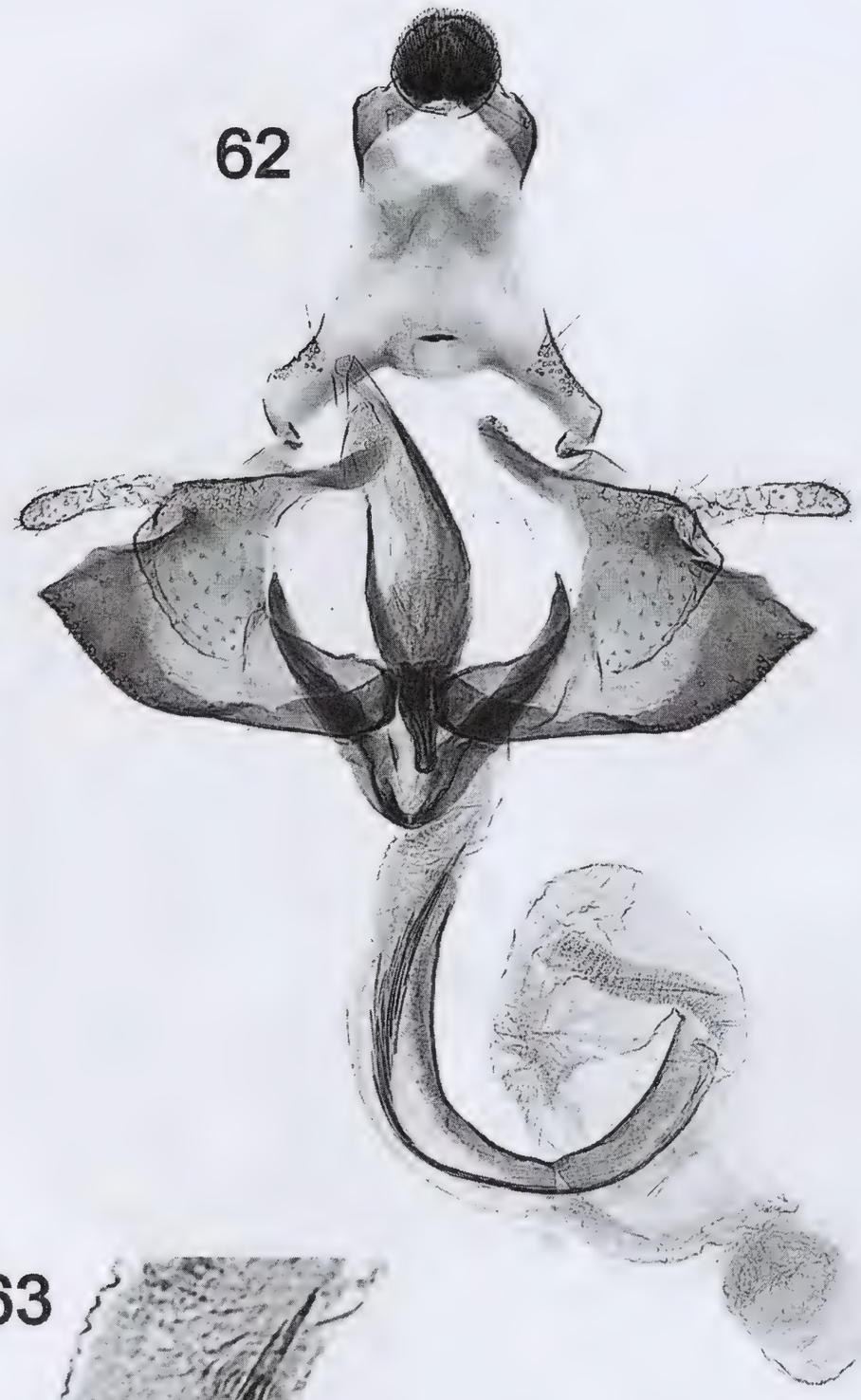
angle and on the dorsal corner a longer horn-shaped protuberance whose apex extends to the apex of the cucullus. Phallotheca with two juxta rods well sclerotized on the dorsal side; the longer is wider in the distal half where there is a robust pointed spine; the shorter rod it is thinner and has a shorter, blunt spine before the apex. There are no cornuti.

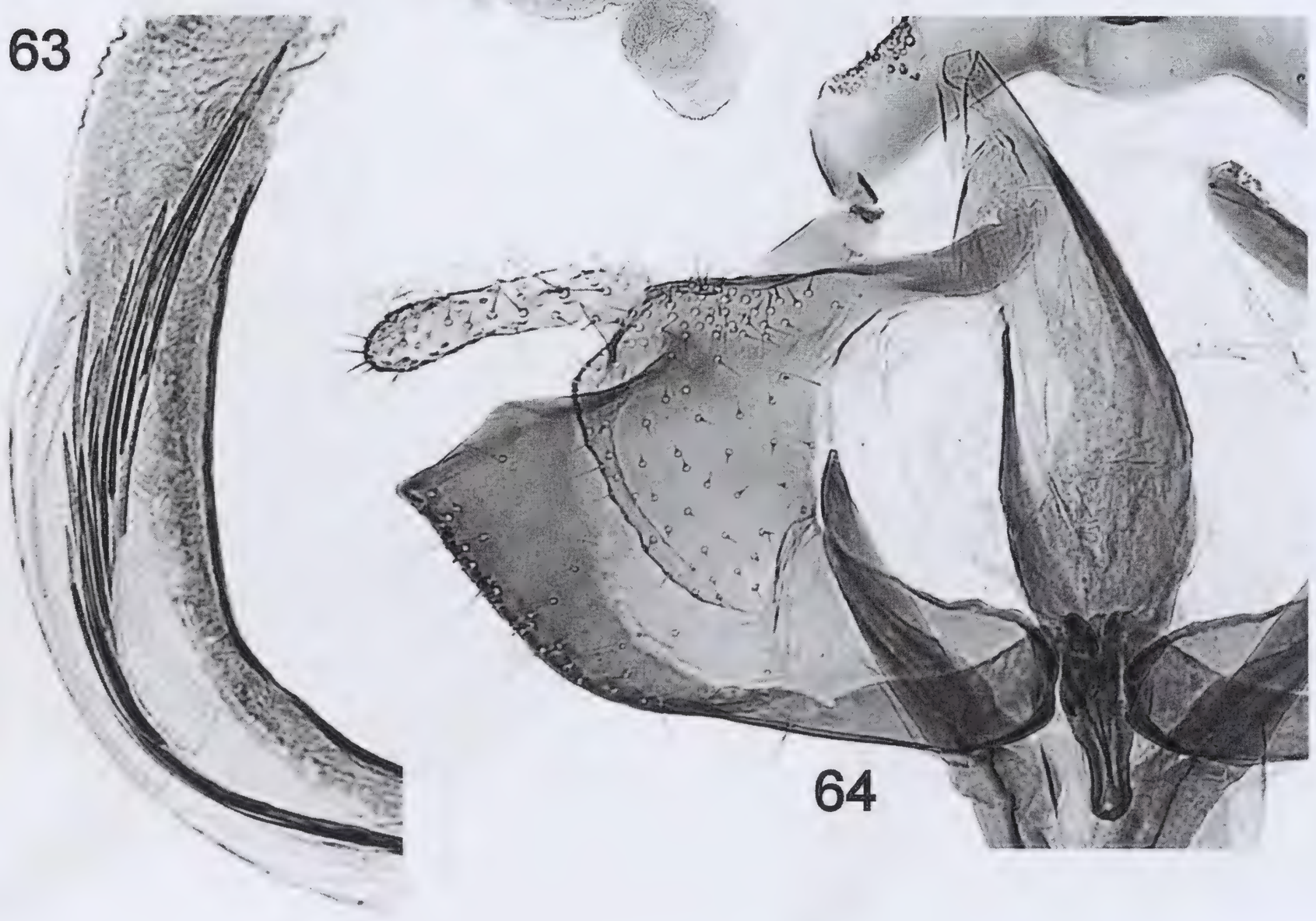
Female genitalia: Unknown.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Kunene).

Etymology: The name derives from the locality where the specimen was collected.





Figs 62-65. Male genitalia of *C. omatakoella* sp. nov. (62) GP Bldz 13526, holotype. (63) Enlarged detail of cornuti. (64) enlarged detail of valva and phallotheca. (65) Abdominal segments 1-5.

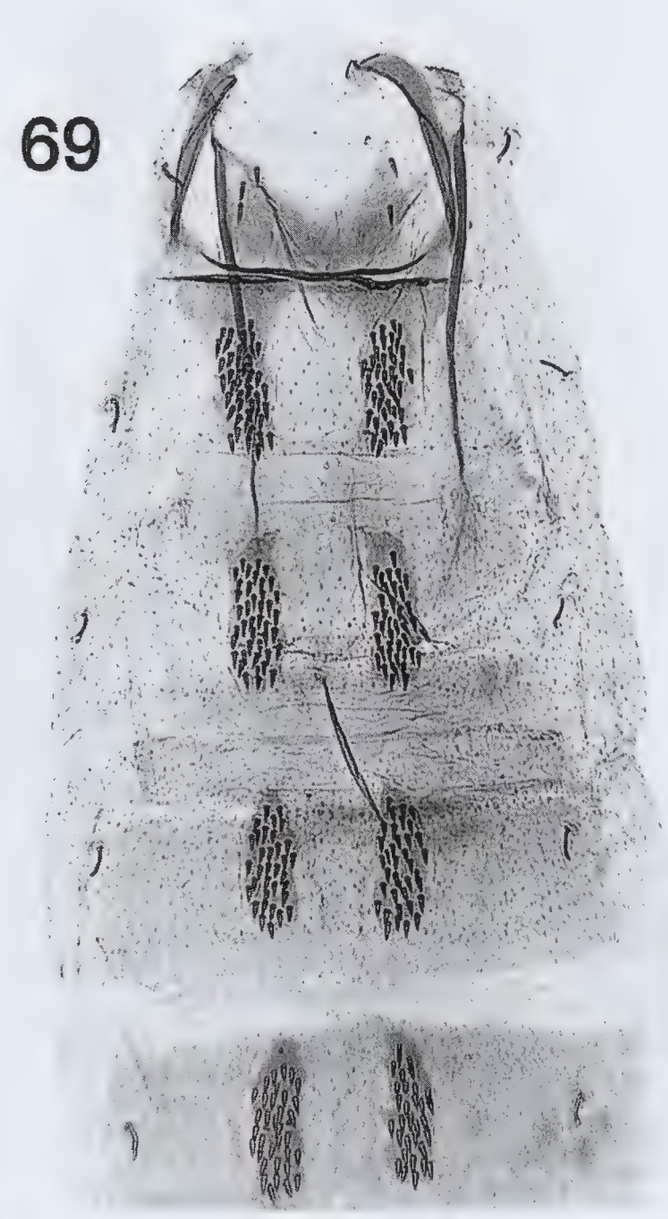
***Coleophora linteella* sp. nov.**
Figs 14, 70-74

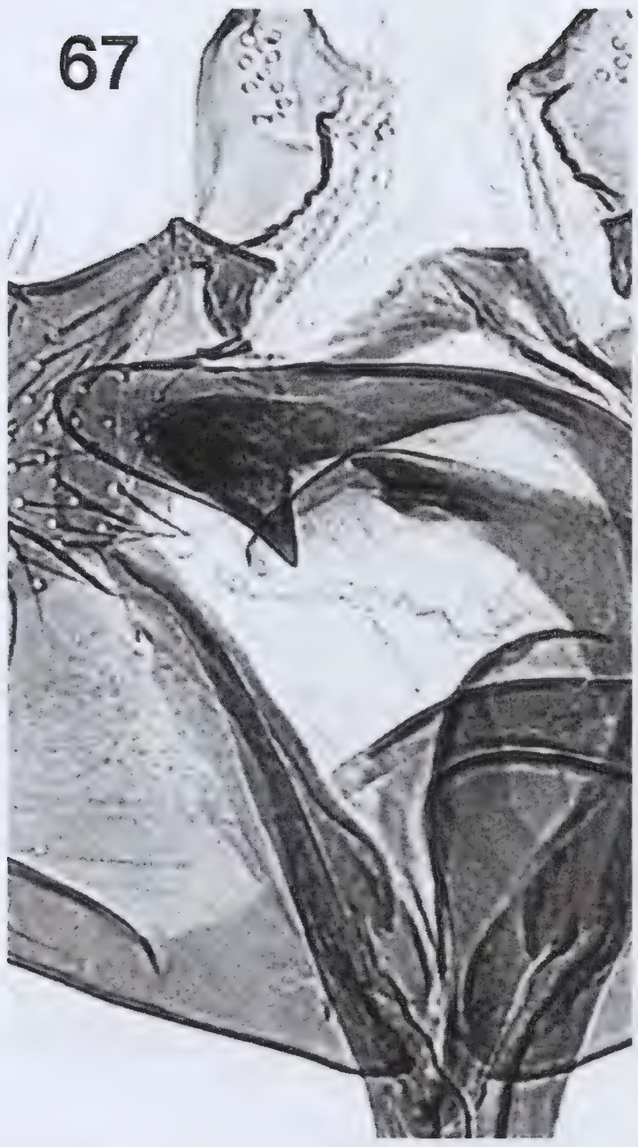
Holotype: ♂ (GP Bldz 15062); "Namibia, Fishriver | Gondwana Canyon Lodge | 13.X.2007 | leg. W. Mey", [27°41.01'S, 7°48.21'E, 850 m]; in coll. MfN.

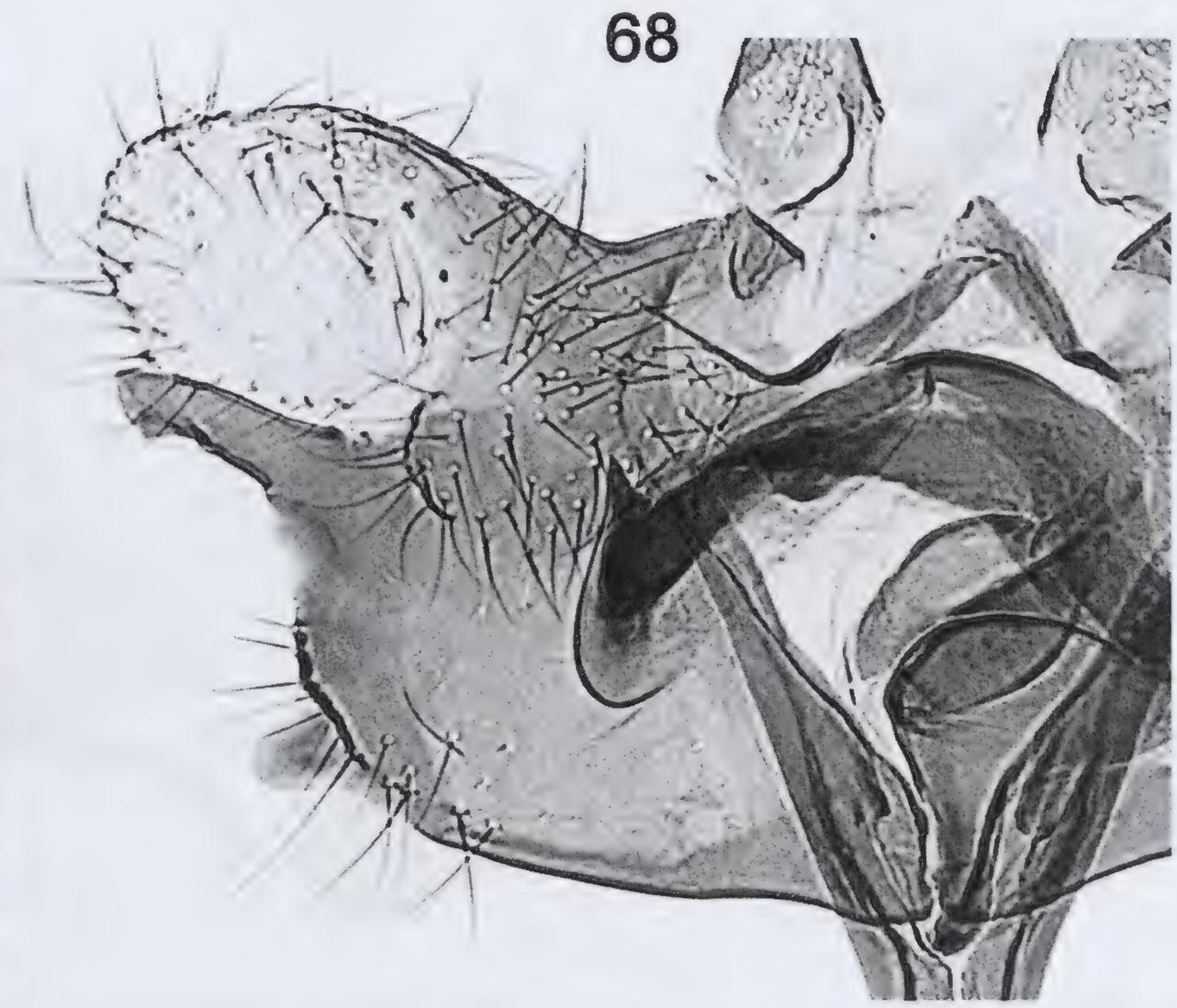
Paratype: 1 ♂ (GP Bldz 15070); "Namibia, Karios | Gondwana Canyon Lodge | 1.XII.2008 | leg. W. Mey", [7°39.185'S, 7°46.476'E, 757 m]; in coll. MfN.

Diagnosis: Species of whitish appearance. The male genitalia does not resemble that of any known afrotropical species, but has some similarities with the Palearctic species *C. arkaimella* Baldizzone & Tabell, 2007, known from Russia (Ural Mts.) with obvious differences in the shape of the cucullus, the sacculus and the phallotheca.

Description: Wingspan 12 mm. Head white. Antenna





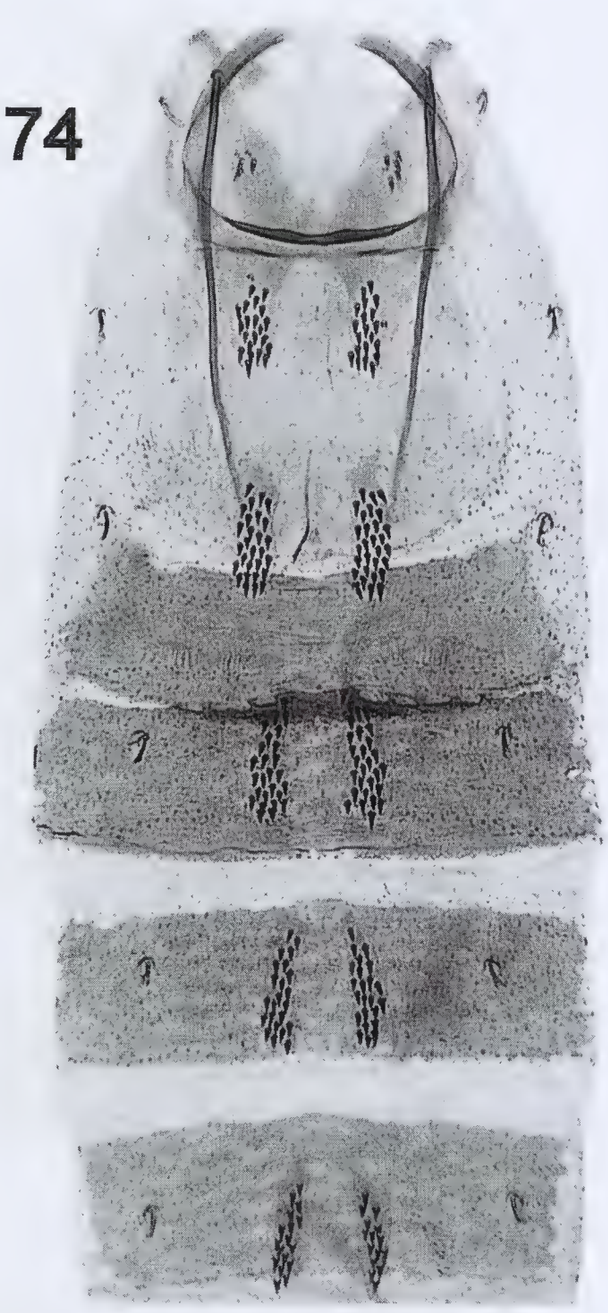


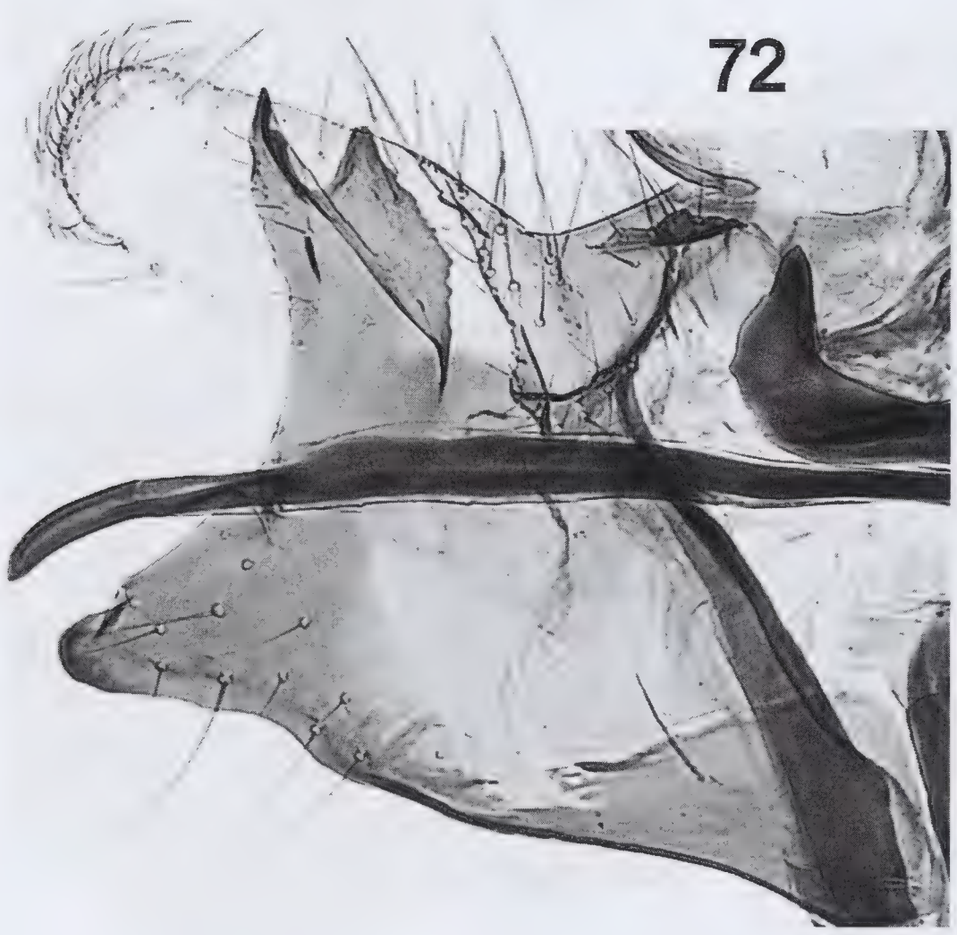
Figs 66-69. Male genitalia of *C. hobaterensis* sp. nov. (66) GP Bldz 14981, holotype. (67) Enlarged detail of phallotheca. (68) GP Bldz 14985, paratype, enlarged detail of valva and phallotheca. (69) GP Bldz 14981, abdominal segments 1-5.

dirty white; scape white, whit a short tuft of erected scales. Labial palpus white; the second segment about 0.5 times longer than the third. Proboscis of normal shape. Thorax and tegula white. Forewing very light ochre scattered whit few brown scales, streaked whit large white lines along the costa, the anal fold and the dorsum; fringes light grey. Hindwing and fringes light grey. Abdomen white.

Abdominal structures (Fig. 74): No posterior lateral struts. Transverse strut with proximal edge curved and thicker and thin distal edge, straight not sclerotized in middle. Tergal disks (3rd tergite) about 3 times as long as wide, covered with about 30 spines.

Male genitalia (Figs 70-73): Gnathos knob oval. Tegumen restricted in middle, pedunculus long, slightly dilated. Transtilla small triangular. Valvula with round ventral

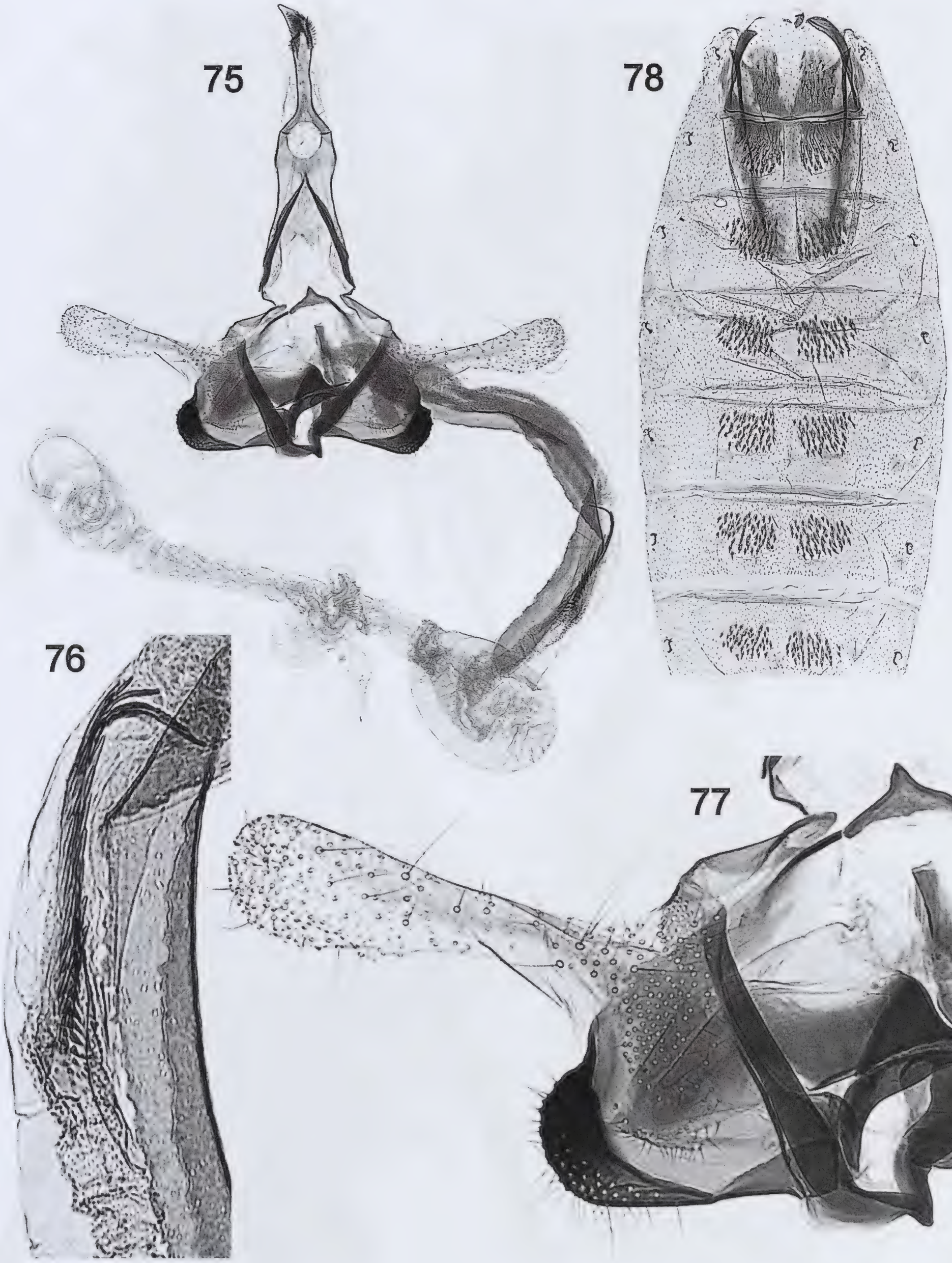




Figs 70-74. Male genitalia of *C. linteella* sp. nov. (70) GP Bldz 15062, holotype. (71) GP Bldz 15070, paratype, enlarged detail of cornuti. (72) GP Bldz 15062, holotype, enlarged detail of valva and phallotheca. (73) GP Bldz 15070, same detail. (74) abdominal segments 1-6.

edge and more sclerotized and a ridge-shaped relief parallel to the upper edge in the dorsal part. Cucullus robust, medium length, slightly wider in the basal half. Sacculus large with a great triangular protuberance in ventral angle and a robust apical protuberance divided into two irregular triangular structures in dorsal angle. Phallotheca with two juxta rods of different length and shape: the longer is thinner, almost straight and ends at the apex with a long slightly curved tip; the other is about half of the first, thicker and ends at the apex with a robust curved tip. Cornuti, two spines of different length joined at the base.

Female genitalia: Unknown.



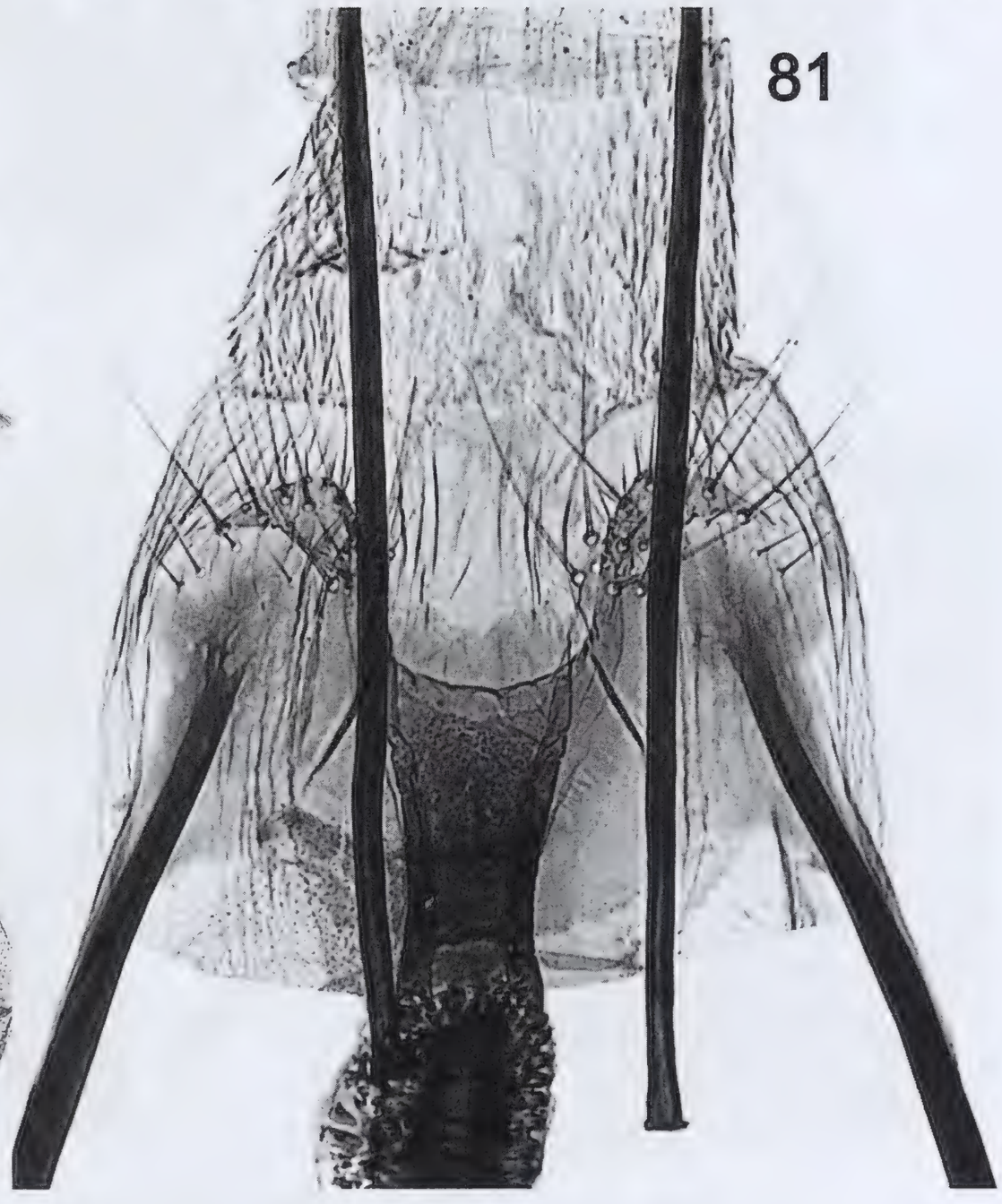
Figs 75-78. Male genitalia of *C. leesi* sp. nov. (75) GP Bldz 16930, paratype. (76) Enlarged detail of cornuti. (77) Enlarged detail of valva and phalloteca. (78) Abdominal segments 1-7.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Karas).

Etymology: The name derives from the Latin *linteus* [*-a, -um*] = linen colour, due to the colour of the forewings.

Remarks: In Fig. 70 the cornuti are broken, which sometimes happens during copula. The complete cornuti are those of Fig. 71.

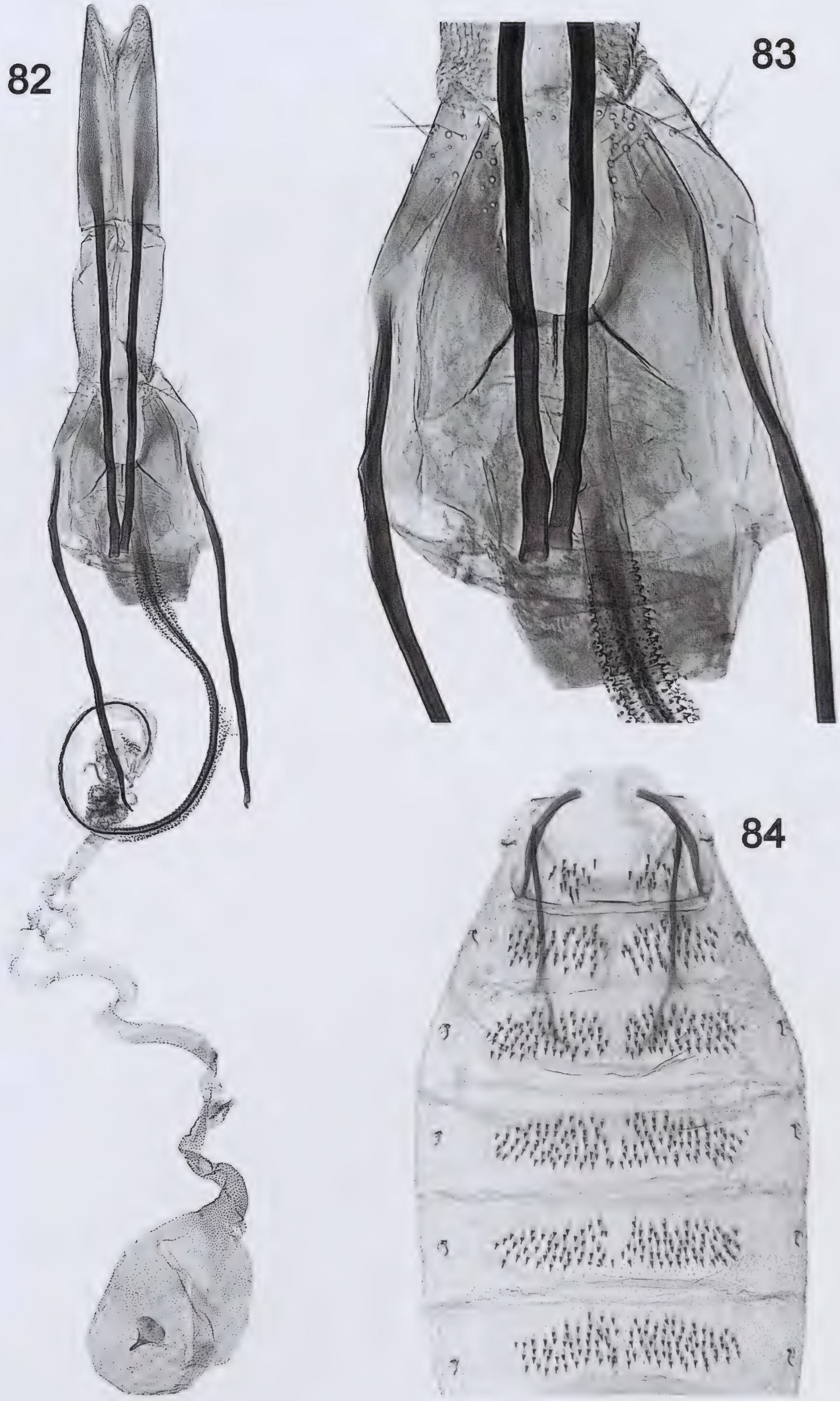


Figs 79-81. Female genitalia of *C. leesi* sp. nov. (79) GP Bldz 16253, paratype. (80) Enlarged detail of sterigma. (81) GP Bldz 16250, paratype, same detail.

***Coleophora leesi* sp. nov.**
Figs 15, 75-81

Holotype: ♂ (GP Bldz 16931) "S. W. AFRICA (W 19) | Sesriem Canyon, Maltahöhe, 2800 ft. | 21-22.i.1972"; "Southern African Exp | B. M. 1972-I";"NHMUK 010897736" [with QR code]; in coll. NHMUK.

Paratypes: 1 ♂ (GP Bldz 16930); "S. W. AFRICA (W 17) | Sesriem Farm | Maltahöhe distr. | 19.-20.i.1972"; Southern African Exp | B. M. 1972-I";"NHMUK 010897633" [with QR code]; in coll. NHMUK. – 1 ♂ (GP Bldz 16257) "Namibia, Solitaire | Tsauchab, camp | 14.4.2013, LF | leg. W. Mey", [24°31.426', 016°.04.391'E, 1042 m]; in coll. MfN. – 4 ♂ (GP Bldz 16248, 16249), 2 ♀ (GP Bldz 16250, 16253); "Namibia, Tiras Mt. | Koiimasis | 8.3.2014 | leg. W. Mey",



Figs 82-84. Female genitalia of *C. spatulifera* sp. nov. (82) GP Bldz 17191, paratype. (83) Enlarged detail of sterigma. (84) Abdominal segments 1-6.

[26°01.25'S, 16°24.01'E, 1280 m]; in coll. MfN and coll. Baldizzone.

Diagnosis: Species of light ochre or whitish appearance. Belongs to the 34° group of Toll (1953, 1962) of which two species of the Afrotropical fauna are known: *C. ugabensis* Baldizzone & van der Wolf, 2004 and *C. hirsutella* Baldizzone & van der Wolf, 2015, both known only from Namibia. The most closely species to *C. leesi* sp. nov. is *C. ugabensis*. In the male genitalia the main differences are: in *C. ugabensis* the gnathos knob is not elongated, larger and rounded, the tegumen is narrower and shorter, the triangular part in middle of the transtilla is smaller, the lateral edge of the sacculus is sclerotized asymmetrically compared

Figs 85-86. Biotopes in which some new species have been collected: (85) Hobatere. (86) Koiimasis. (photos W. Mey)

to that of *C. leesi* sp. nov., there are no cornuti. In the female genitalia the differences are less evident: in *C. ugabensis* the sterigma is lower, the colliculum is narrower, the anterior part of the ductus bursae is thinner, the corpus bursae is slightly smaller.

Description: Wingspan 13-14 mm. Head white, light ochre suffused dorsally. Antenna light ochre, sometimes ringed brown on the distal half; scape white, with a tuft of erected scales, white on outer side, ochraceous ferruginous on inner side. Labial palpus very short, white, ochre suffused on outer side; the second segment about 0.5 times longer than the third. Proboscis of normal shape. Thorax and tegula white, light ochre suffused. Forewing light ochre or whitish, scattered

Figs 87-88. Biotopes in which some new species have been collected: (87) Erichsfeld. (88) Karios. (photos W. Mey)

from few light brown scales at the apex; fringes light ochre. Hindwing light grey; fringes light ochre. Abdomen whitish.

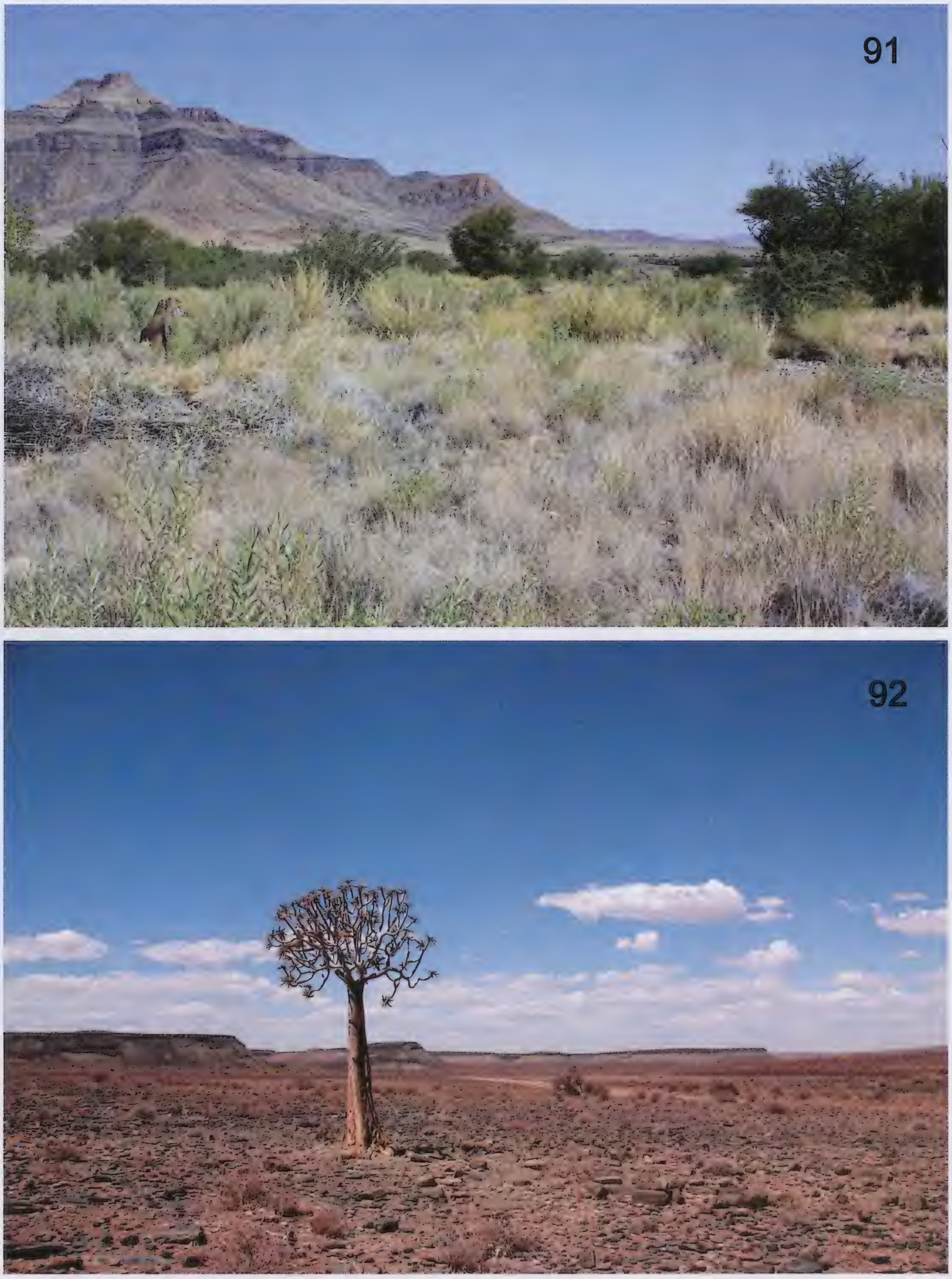
Abdominal structures (Fig. 78): No posterior lateral struts. Transverse strut slender, slightly curved. Tergal disks (3rd tergite) large about twice their length, covered with about 50 little conical spines with large base.

Male genitalia (Figs 75-77): Gnathos knob thin, elongated beak-shaped, covered with spines only on the dorsal side. Tegumen long, slightly restricted in middle; pedunculus moderately dilated. Transtilla thin, joined in middle in a triangular large structure. Valvula big, covered by short setae, with lower edge rounded. Cucullus elongated, restricted at 1/3 from the base,

Figs 89-90. Biotopes in which some new species have been collected: (89) Omatako. (90) North of Solitaire. (photos W. Mey)

club-shaped. Sacculus small, very sclerotized on the outer edge, curved, slightly jagged. Phallotheca large, conical, with two almost completely fused symmetrical juxta rods, more sclerotized at the base and in the distal half. Cornuti: many spines of different length, joined in a formation similar to a long claw.

Female genitalia: (Figs 79-81) Papillae anales small and oval. Apophyses posteriores about as long as the anteriores. Tuba analis covered with small spines. Sterigma trapezoidal, little sclerotized, largely hollowed by the sinus vaginalis, curved dorsal edge with long setae. Ostium bursae large, oval. Colliculum cup-shaped,



Figs 91-92. Biotopes in which some new species have been collected: (91) Tsauchab valley (photo W. Mey). (92) Fishriver canyon (photo G. Bassi).

more sclerotized on the outer sides. Ductus bursae long: posterior part, with long medial line, completely wrapped in two sclerotized bands covered with triangular spines; anterior part more transparent with some convolutions of various sizes. Corpus bursae large, spherical, with a leaf-shaped signum.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Karas).

Etymology: The species is dedicated to David C. Lees, curator of Microlepidoptera at NHMUK in recognition of his research on Afrotropical microlepidoptera especially of Madagascar.

Coleophora spatulifera sp. nov.

Figs 16, 82-84

Holotype: ♀ (GP Bldz 15057); "RSA | 50 km NE Bitterfontein | Drai-Hoek | 25.XI.2008 | leg. Ebert, Kühne & W. Mey, LF", [30°42'S 18°25'E]; in coll. MfN.

Paratypes: 1 ♀ (GP Bldz 16265); "Namibia, Gobabeb | Kuiseb-Tal | LF | 16.-19.1.2007 | leg. Mey & Ebert", [23°52.58'S 15°04.28'E, 373 m]; in coll. MfN. – 6 ♀ (GP Bldz 17187); "Namibia, Gamsb. | Rooiklip Farm | 22.-24.11.2007, LF | leg. W. Mey", [23°24.382'S, 16°03.614'E, 1075 m]; in coll. MfN and coll. Baldizzone. – 1 ♀ (GP Bldz 17154); same locality as previous, 6.-7.XI.2019, leg. W. Mey, coll. MfN. – 2 ♀ (GP Bldz 17191); same locality as previous, 6.-7. XI.2019, LF | leg. W. Mey; in coll. MfN.

Diagnosis: Species with habitus completely white. The male is unknown. On the basis of the female genitalia and tergal disks, it belongs to the group of Afrotropical species similar to *C. ugabensis* Baldizzone & van der Wolf, 2004, from which it clearly differs in the shape of the large papillae anales, the large sterigma and the thin ductus bursae. Its structure is more similar to that of numerous palearctic species described by Falkovitsh, in example *C. tytri* Falkovitsh, 1970, *C. dilabens* (Falkovitsh, 1982), *C. crassa* (Falkovitsh, 1989); in addition to the differences in sterigma and ductus bursae, the most evident is the very characteristic large and elongated papillae anales.

Description: Wingspan 10-12 mm. Head white. Antenna white ringed brown in the distal third; white scape with a short tuft of erected scales. Labial palp white, the second article is about twice as long as the third. Proboscis of normal shape. Thorax and tegula white. Forewing white, slightly tinged light ochre; costal fringes white, dorsal fringes light grey. Hindwing and fringes light grey. Abdomen white.
Abdominal structures (Fig. 84): No posterior lateral struts. Transverse strut slender, slightly curved. Tergal disks (3rd tergite) large about 2,5-3 times their length, covered with about 60 little, slender spines with large base.
Male genitalia: Unknown.
Female genitalia (Figs 82, 83): Papillae anales very long, well sclerotized, spatula-shaped. Apophyses posteriores about as long as the anteriores. Sterigma suboval, about twice long as large, more sclerotized in the anterior part, deeply hollowed by the sinus vaginalis. Ostium bursae broad, oval. Colliculum narrow and elongated calyx-shaped. Ductus bursae long: posterior part thin, wrapped by two bands covered with small spines, except in the central convolution where only the medial line is present; anterior part wider, transparent, finely dotted, with some convolutions of various sizes. Corpus bursae thickly dotted, oval sac shaped, with a small signum in the shape of a leaf.

Bionomy: The early stages and the foodplant are unknown.

Distribution: Namibia (prov. Swakopmund, Erongo; Windhoek, Khomas) and RSA (prov. Northern Cape).

Etymology: The name derives from the Latin words *spatula* = spatula, and *fero* [*fĕrs, tuli, latum, fĕrre*] = to bear, due to the characteristic shape of the papillae anales.

LIST OF COLEOPHORA SPECIES OF NAMIBIA

The names are listed here in alphabetical order (Baldizzone & van der Wolf, 2004, 2011, 2015):

C. afrotropicalis Baldizzone & van der Wolf, 2004
C. abstrusa sp. nov.
C. albadomina Baldizzone & van der Wolf, 2004
C. amaurosella sp. nov.
C. aquaecadentis Baldizzone & van der Wolf, 2004
C. arens Baldizzone & van der Wolf, 2004
C. ausensis sp. nov.
C. austrina Baldizzone & van der Wolf, 2004
C. brandbergella Baldizzone & van der Wolf, 2004
C. capricornis Baldizzone & van der Wolf, 2004
C. *damarella* Baldizzone & van der Wolf, 2004
C. demiranda sp. nov.
C. etoshae Baldizzone & van der Wolf, 2011
C. exotica sp. nov.
C. gondwanae sp. nov.
C. hirsutella Baldizzone & van der Wolf, 2015
C. hobaterensis sp. nov.
C. jurateella Baldizzone & van der Wolf, 2011
C. kamiesella Baldizzone & van der Wolf, 2015
C. karischella Baldizzone & van der Wolf, 2011
C. kruegeri Baldizzone & van der Wolf, 2004
C. kunenensis Baldizzone & van der Wolf, 2015
C. leesi sp. nov.
C. linteella sp. nov.

C. magnaefontis sp. nov.
C. meyi Baldizzone & van der Wolf, 2004
C. mirabibella Baldizzone, Mey & van der Wolf, 2011
C. monticola Baldizzone & van der Wolf, 2004
C. namella Baldizzone & van der Wolf, 2004
C. namibiae Baldizzone & van der Wolf, 2004
C. omatokella sp. nov.
C. oxyphaea Meyrick, 1913
C. pectinella sp. nov.
C. presbytica Meyrick, 1911
C. sandveldensis sp. nov.
C. sanella Baldizzone & van der Wolf, 2004
C. scaleuta Meyrick, 1911
C. spatulifera sp. nov.
C. textoria Meyrick, 1921
C. ugabensis Baldizzone & van der Wolf, 2004
C. vansoni Baldizzone & van der Wolf, 2015

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I am warmly grateful to Wolfram Mey (MfN, Berlin, Germany) who sent me most of the specimens that allowed the realization of this work. I also thank Alessandro Giusti for the loan of NHMUK specimens and for various information. My thanks also extend to Graziano Bassi (Avigliana, Italy) for the loan and gift of specimens that he collected. Many thanks to Pier Giuseppe Varalda (Morano sul Po, Italy) for photographing spread specimens. Finally, many thanks to Terence Hollingworth (Blagnac, France), who revised and corrected the English text and to Bernard Landry (Geneva, Switzerland) for revision of the text, corrections and useful advice and to the anonymous reviewers for their comments and suggestions.

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Baldizzone G., van der Wolf H.W. 2020a. On the taxonomy of Afrotropical Coleophoridae (III). New or little known species from Central and Oriental Africa (Lepidoptera, Coleophoridae) *Zootaxa* 4763: 151-174. DOI: 10.11646/zootaxa.4763.2.1

Baldizzone G., van der Wolf H.W. 2020b. On the taxonomy of Afrotropical Coleophoridae (IV). New or little known species from South Africa (Lepidoptera, Coleophoridae) *Zootaxa* 4816(2): 151-170. DOI: 10.11646/zootaxa.4816.2.1

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First record of *Phallocaecilius* Lee & Thornton, 1967 (Psocodea: 'Psocoptera': Pseudocaeciliidae) from India, with the description of a new species from the Southern Western Ghats

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Abstract: *Phallocaecilius indicus* sp. nov., from the Southern Western Ghats of Tamil Nadu and Kerala, India, is here described and illustrated. This is the third known species in the genus, which is here reported from the Indian subcontinent for the first time.

Keywords: New species - barklice - taxonomy - Agasthiyamalai Biosphere Reserve - Meghamalai.

INTRODUCTION

Lee & Thornton (1967) erected the genus *Phallocaecilius*, with *P. hirsutus* (Thornton, 1961) from Hong Kong as the type species. The genus is characterized by the presence of sense-papillae in the anal area of the male forewing, a hypandrium with lateral sclerites, a long endophallus with thorn-like sclerites, a bilobed subgenital plate, small gonapophyses, and the ventral and dorsal valves unlobed and membranous (Lee & Thornton, 1967). Two species of this genus are known: *P. hirsutus* (Thornton, 1961) [Hong Kong] and *P. sentosus* Li, 1999 [China]. Their distribution is restricted to the Asia and Pacific regions (Hong Kong, China, Christmas Island, Indonesia, Japan); so far, the genus has not been recorded from the Indian subcontinent (Yoshizawa, 1996; Lienhard & Smithers, 2002; New & Lienhard, 2007). Here we describe a new species of *Phallocaecilius* from the Southern Western Ghats of Tamil Nadu and Kerala, India.

MATERIALS AND METHODS

The specimens were collected in an enamel tray by beating dead leaves and green vegetation near streams in different parts of Tamil Nadu and Kerala, India and stored in vials with 70% ethanol (Fig. 1). External morphology and color pattern of the specimens were studied by placing whole specimens under a stereo zoom microscope (Leica M205A) and photographed using Leica Application Suite. The body parts (head, lacinia, legs, wings and genitalia) of fifteen specimens were dissected and mounted in Canada balsam. The remaining parts of the dissected specimens are preserved in 70% ethanol for further studies. The mounted body parts were observed, measured and photographed under a compound microscope (Leica DM3000). Illustrations were made using Clip Studio Paint Pro software and edited with Adobe Photoshop CS5. The terminology for body parts follows Yoshizawa (2005) and New & Lienhard (2007). The studied specimens are deposited in the following institutions: National Zoological Collections of the Southern Regional Centre, Zoological Survey of India, Chennai, Tamil Nadu, India (SRC/ZSI) and Western Ghats Regional Centre, Zoological Survey of India, Kozhikode, Kerala (WGRC/ZSI).

Abbreviations used in the descriptions and measurements are as follows: FWL, HWL: lengths of right fore- and hindwings; F, T, t1, t2: lengths of femur, tibia, and tarsomeres 1, and 2 of right hind leg; Mx4: length of the fourth segment of right maxillary palpus; ctt1: number of ctenidobothria on t1; f1...fn: lengths of flagellomeres 1...n of right antenna; IO, D, d: minimum distance between compound eyes, antero-posterior diameter, and transverse diameter of right compound eye, respectively, all in dorsal view of head; PO: d/D; measurements are in μm.

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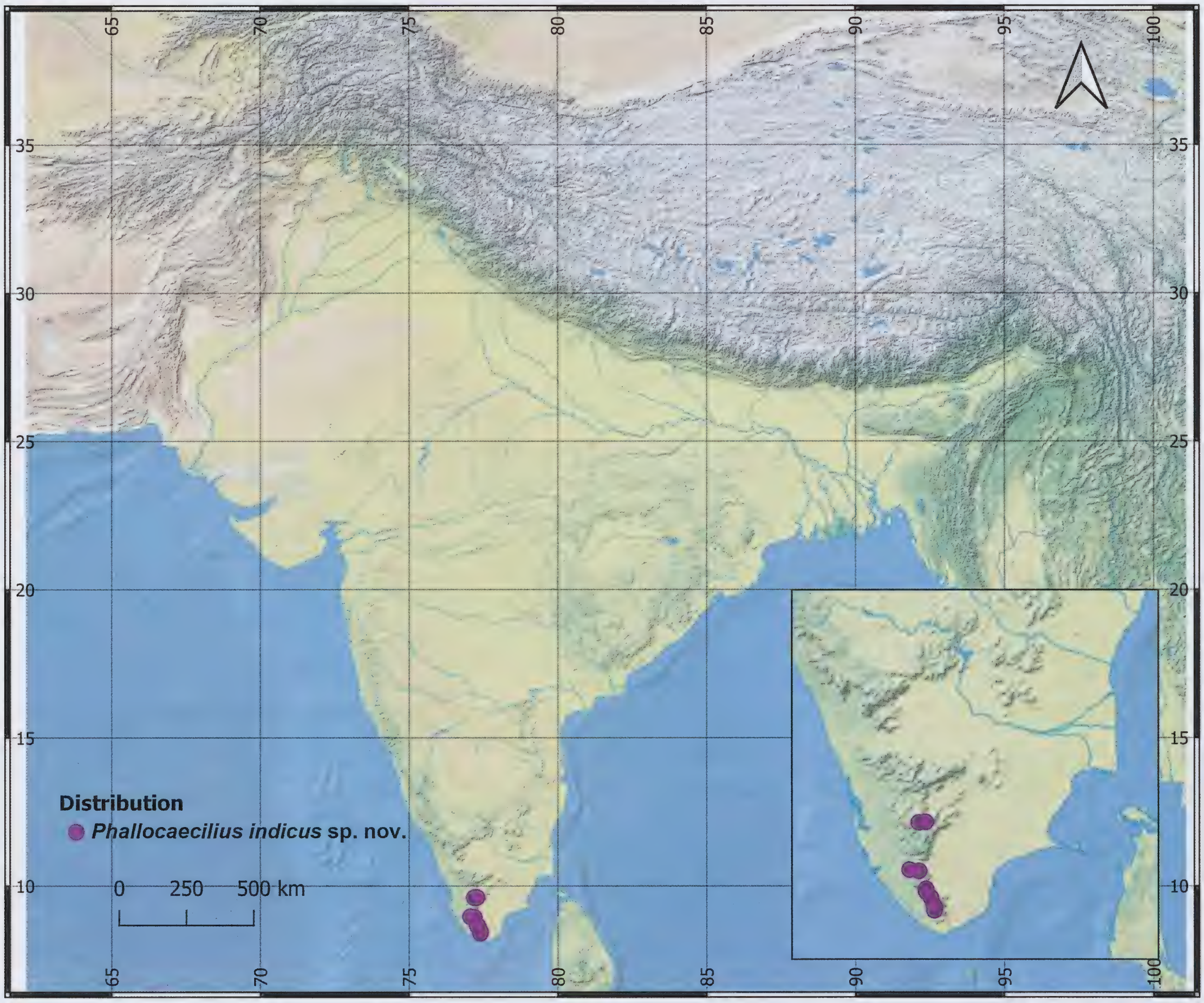


Fig. 1. Distribution records of *Phallocaecilius indicus* sp. nov. in the Southern Western Ghats.

TAXONOMIC PART

***Phallocaecilius indicus* sp. nov.**

Figs 2-17

Material examined

Holotype: SRC-ZSI/I/PSO/78; male (Slide mounted); India, Tamil Nadu, Tirunelveli District, Agasthiyamalai Biosphere Reserve, Kalakkad-Mundanthurai Tiger Reserve (KMTR), Ambasamudram Range, Kuthiraivetti, 8.58790° N, 077.34141° E, 1231 m; 22.08.2019; leg. R. Babu.

Paratypes: SRC-ZSI/I/PSO/79 to SRC-ZSI/I/PSO/92 and ZSI/WGRC/I.R.- INV.18308 (slide-mounted, or in 70% ethanol); 19 males, 24 females, same data as the holotype. 1 male, 10 females; Tamil Nadu, Tirunelveli District, Kalakkad-Mundanthurai Tiger Reserve, Mundanthurai Range, Karaiyar Beat, Gouthalaiaru, 8.66766° N, 077.27757° E, 289 m; 18.08.2019; leg. R. Babu. 3 males, 15 females; Tamil Nadu, Tirunelveli District, Kalakkad-Mundanthurai Tiger Reserve, Mundanthurai Range, Servalar, Kodamadi, 8.70349° N, 077.27581° E, 440.6 m; 19.08.2019; leg. R. Babu. 1 male, 18 females; Tamil Nadu, Kanyakumari District, Kanyakumari Wildlife Sanctuary, Kalikesam, 8.410000° N, 77.389367° E, 124 m; 04.12.2018; leg. J. Thilak. 2 males, 13 females; Tamil Nadu, Kanyakumari Wildlife Sanctuary, Alagiyapandiyapuram Range, Balamore, 8.455683° N, 77.391417° E, 450 m; 04.12.2018; leg. J. Thilak. 5 females; Tamil Nadu, Kanyakumari Wildlife Sanctuary, on the way to Muthukulivayal, 2nd bend, 08.47609° N, 077.38336° E, 994 m; 16.02.2020; leg. Varadaraju. 1 male, 12 females; Tamil Nadu, Theni District, Meghamalai Wildlife Sanctuary, Gudalur Range, Vannathiparai, 9.61901° N, 77.27161° E, 504 m; 28.02.2019; leg. R. Babu. 9 males, 11 females; Tamil Nadu, Theni District, Meghamalai Wildlife Sanctuary, Gudalur Range, Amaravathi Beat, Bublimash Stream, 9.61103° N, 77.17855° E, 891 m; 01.03.2019; leg. R. Babu. 6 males, 3 females; Kerala, Agasthiyamalai Biosphere Reserve, Shendurney Wildlife Sanctuary,

Kollam District, Rosemala, 8.949933° N, 77.180500° E, 555 m; 22.01.2019; leg. G. Ramesh. 5 males; Kerala, Agasthiyamalai Biosphere Reserve, Shendurney Wildlife Sanctuary, Kollam District, Deer Park, Thenmala, 8.966522° N, 77.052261° E, 91 m; 23.01.2019; leg. G. Ramesh.

Diagnosis: *Phallocaecilius indicus* sp. nov., differs from the other known species, *P. hirsutus* and *P. sentosus* by the male phallosome endophallus having stout, spine like (like hard stout spines) thorn sclerites; in females, the subgenital plate apical lobes bear one seta apically and another one on the mesial border, gonapophyses ventral valves narrow, pointed apically; dorsal valves with broad lobe, bearing a bristled stylet; external valves rounded, apically thin, bearing four long setae. In the other two species, the phallosome endophallus bears less robust thorns. In the female of *P. hirsutus,* the apical lobe of the subgenital plate bears five to six setae, external valves triangular, dorsal valves bulged and ventral valves fleshy or membranous.

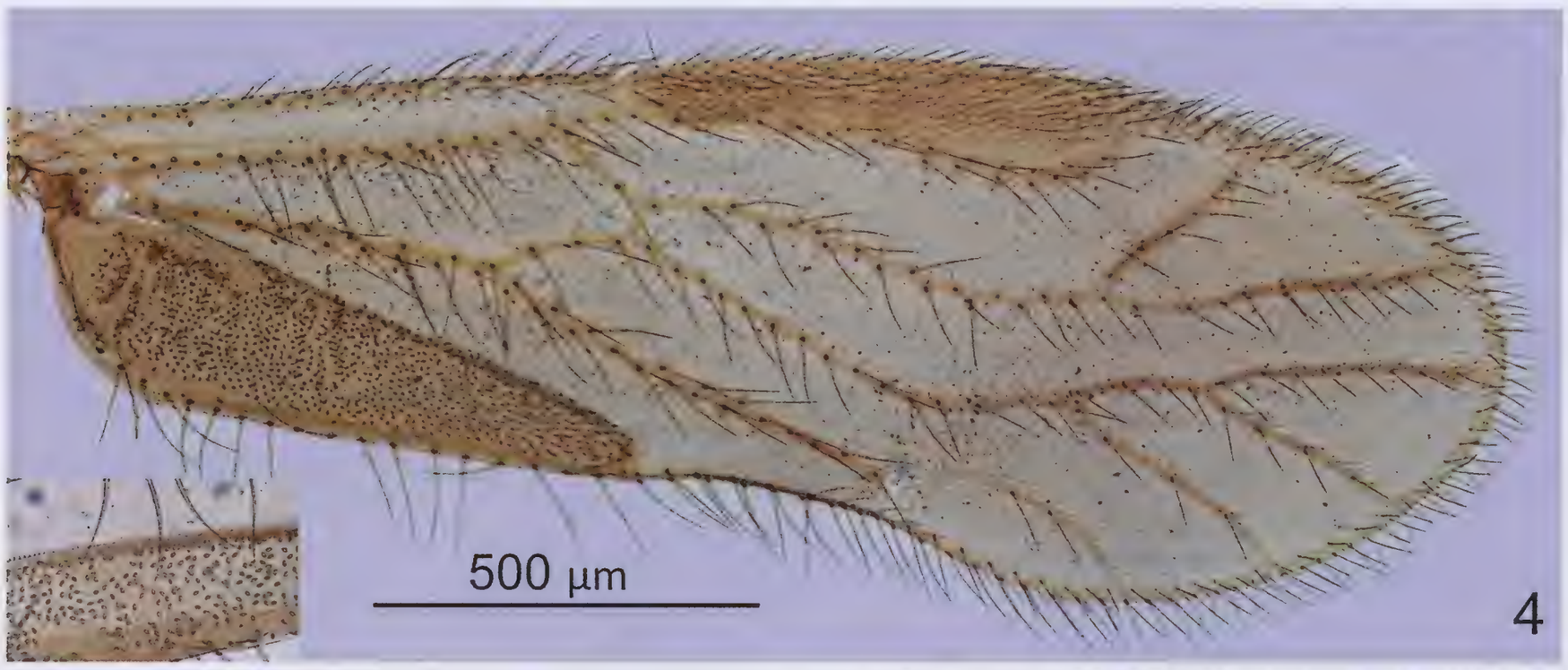
Etymology: The species epithet refers to the country name India.

Description of the male holotype

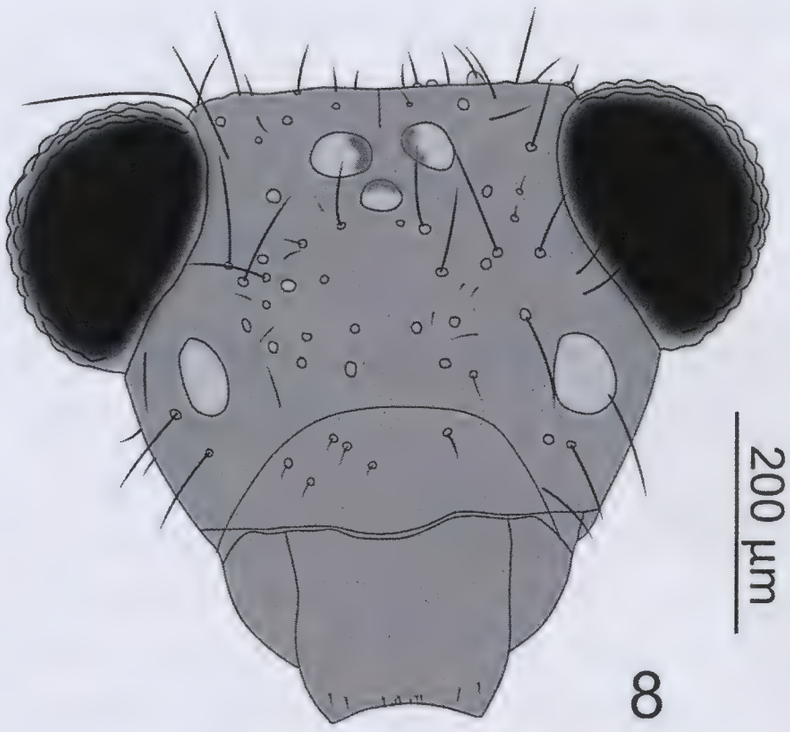
Color: Vertex and frons yellowish-brown, ocelli hyaline, with conspicuous reddish-brown centripetal crescents, genae pale yellowish, eyes brownish-black, third and fourth maxillary palpomeres slightly brown, clypeus yellowish-brown, antenna buff, scape and pedicel light brown. Prothorax pale yellowish, meso- and metathorax light brown. Forewings brown, veins brown except for M+Cu1, R2+3, R4+5, M1 and M2 light brown. Hindwings hyaline, veins pale yellow except M+Cu1, Rs and proximal Cu1 light brown. Legs: femora, tibiae and tarsi light brown, claws brown. Abdomen yellowish brown (Fig. 2).

General morphology: Body length 1.8-2.1 mm. Frons and vertex bearing stout black setae, compound eyes small, three ocelli, in triangular arrangement (Fig. 8), fourth maxillary palpomere apically rounded, setose.

Figs 2-3. *Phallocaecilius indicus* sp. nov. (2) Male habitus. (3) Female habitus.



Figs 4-7. *Phallocaecilius indicus* sp. nov. (4-5) Male forewing and hindwing. (6-7) Female forewing and hindwing.



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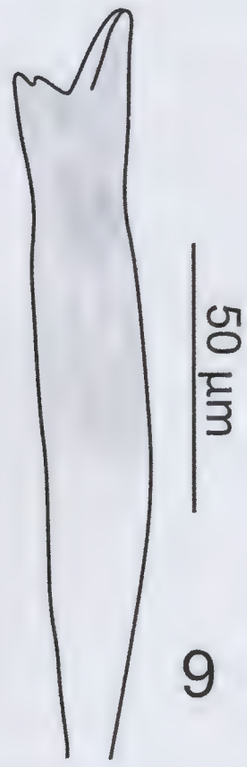

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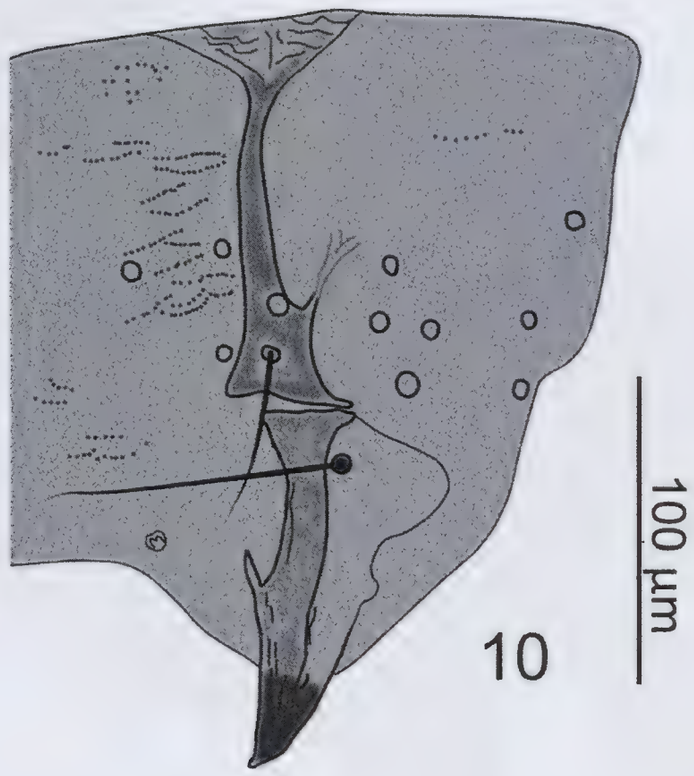

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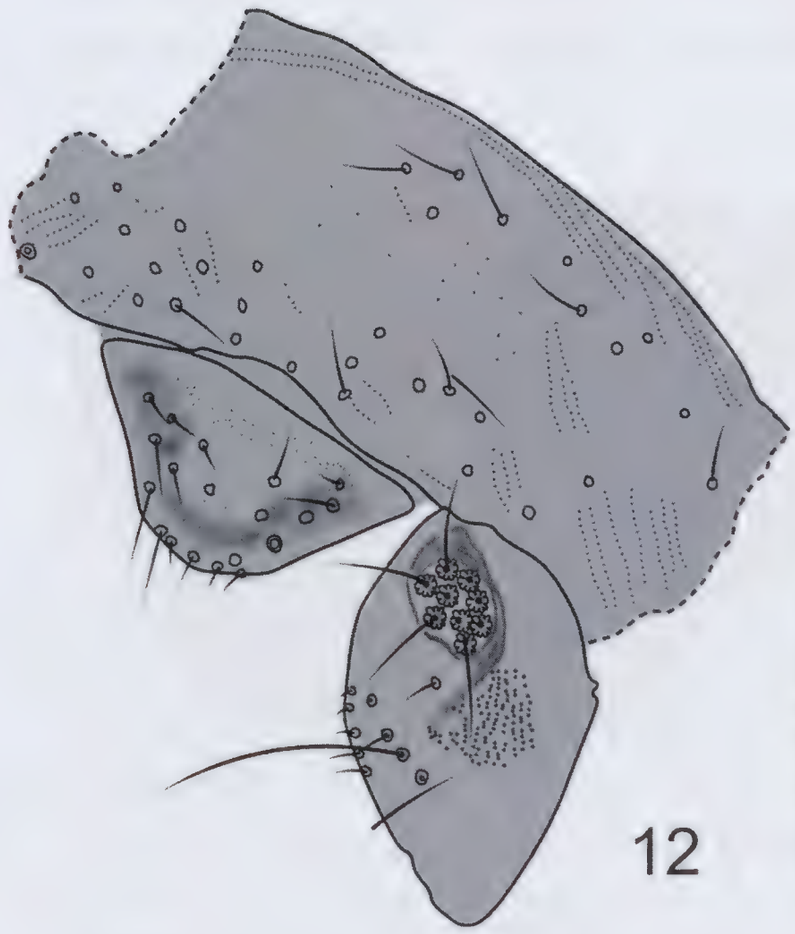

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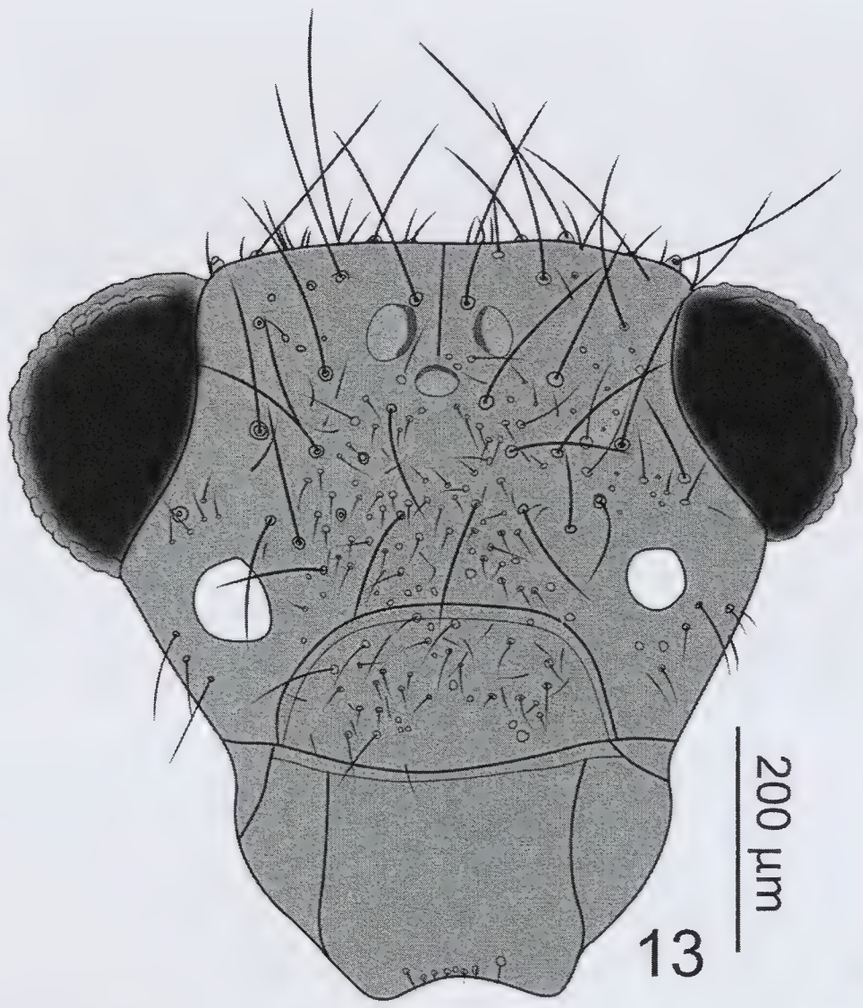
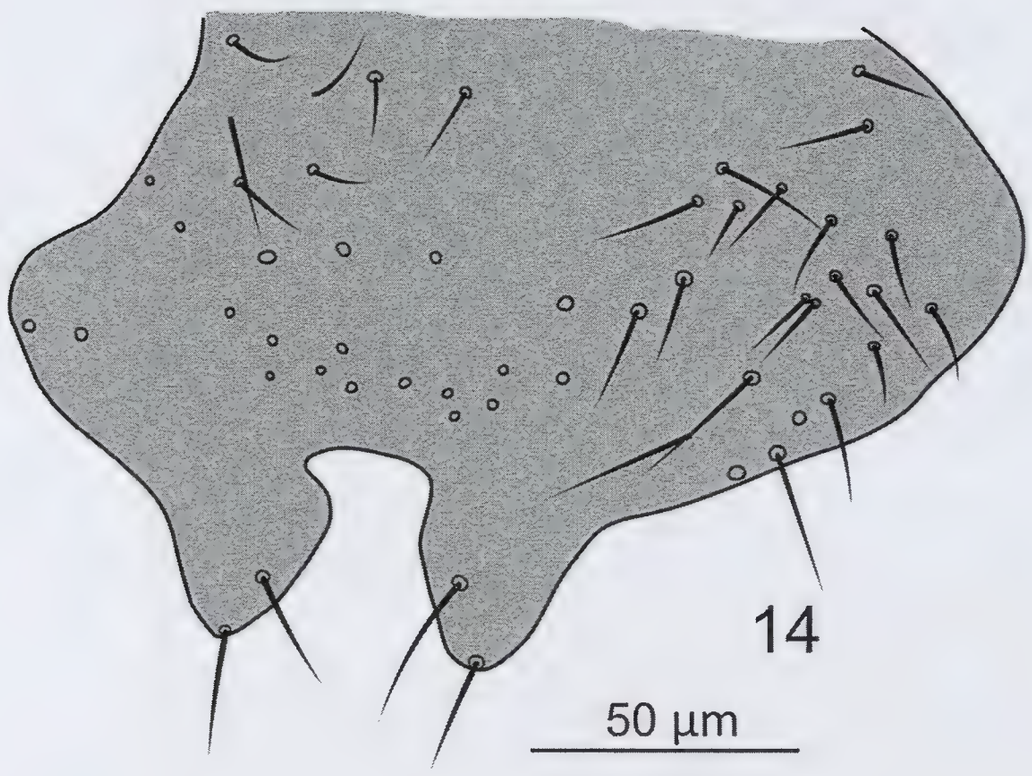
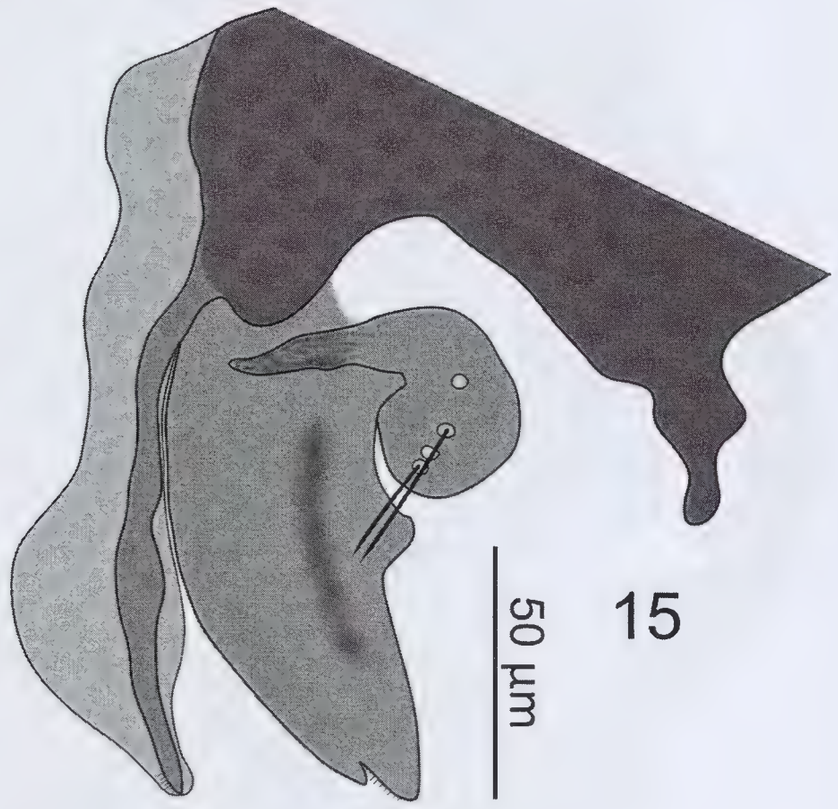
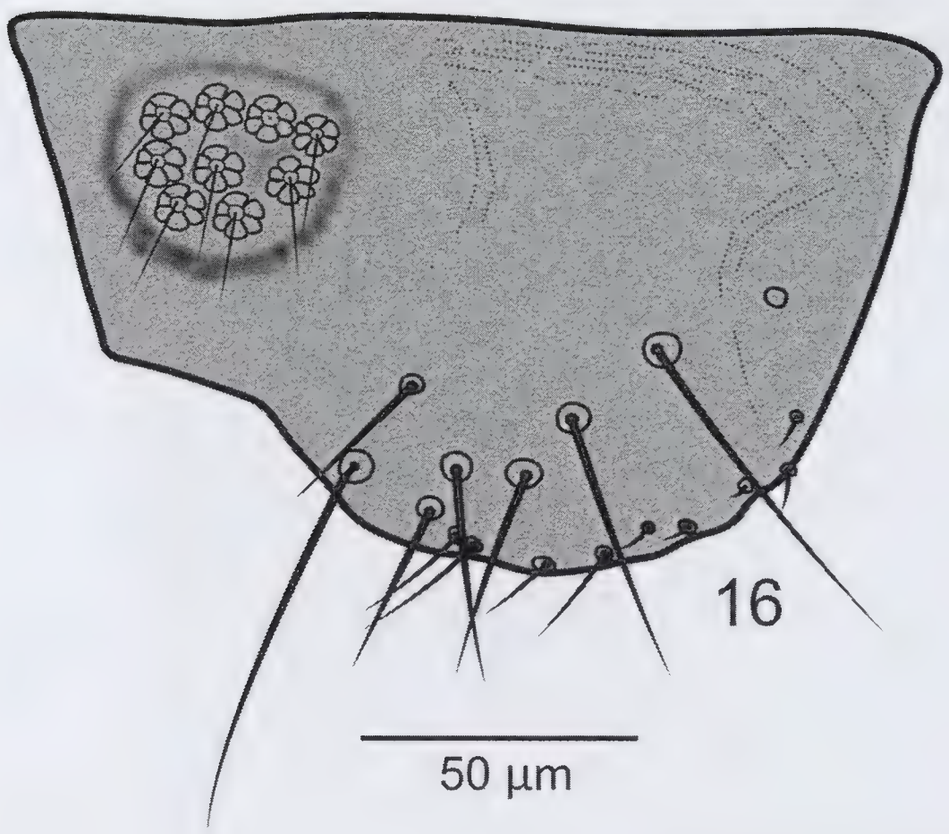
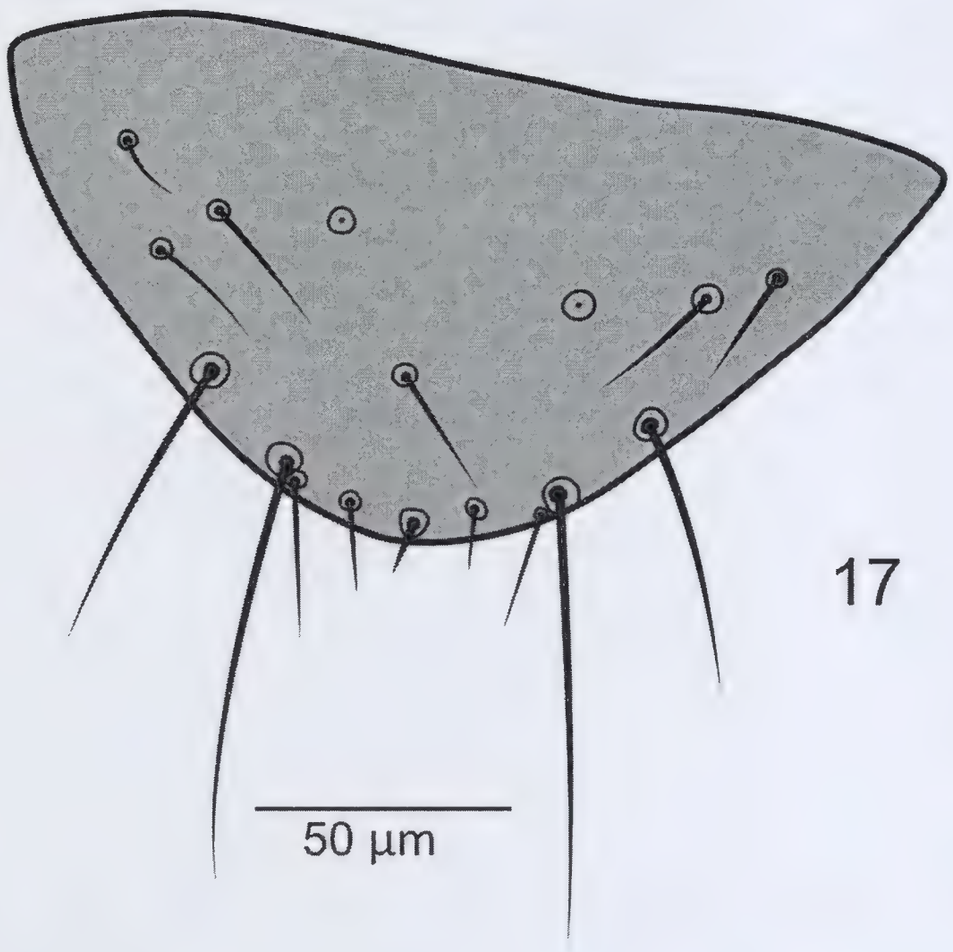
Figs 8-12. *Phallocaecilius indicus* sp. nov. Male. (8) Front view of head. (9) Right lacinia. (10) Hypandrium. (11) Phallosome. (12) Clunium, epiproct and paraproct.











Figs 13-17. *Phallocaecilius indicus* sp. nov. Female. (13) Front view of head. (14) Subgenital plate. (15) Gonapophyses. (16) Right paraproct. (17) Epiproct.

Lacinia as in Fig. 9. Forewings: veins and wing margin setose, Rs and M joined by a cross vein, pterostigma long and narrow, cells of 1a and cu2 covered with sensory papillae, areola postica flattened (Fig. 4). Hindwing membrane and veins smooth, outer margin with dense setose except for ¾ of basal coastal margin glabrous (Fig. 5). Claws without preapical teeth, apically slightly curved, ribbon-like pulvillus.

Genitalic characters: Hypandrium: simple, setose, with lateral sclerites and sclerotized in apical lateral sclerites (Fig. 10). Phallosome: lateral projection at a basal angle of phallobase, parameres strongly arched, aedeagus strongly sclerotized, endophallus expanded with many thorn-like (like hard stout spines) sclerites (Fig. 11). Epiproct and paraprocts as illustrated (Fig. 12).

Description of the female allotype

Color: Same as in the male (Fig. 3).

General morphology: Body length 1.9-2.2 mm. Similar to the male, but sensory papillae absent in the cells 1a and cu2 in forewing (Fig. 6). Hindwing similar to that in the male (Fig. 7).

Genitalic characters: Subgenital plate: with apically deep indentation, apical lobe well developed, bilobed, each lobe bearing an apical seta and another on mesial border. The rest of the plate setose (Fig. 14). Gonapophyses: ventral valves narrow, apically pointed; dorsal valves with broad lobe, bearing a bristled stylet; external valves rounded, apically thin, bearing four long setae (Fig. 15). Paraprocts with fields of 9-10 trichobothria, bearing a row of apical and subapical setae (Fig. 16). Epiproct triangular, with two long setae latero-apically and five small setae distally (Fig. 17).

Dimensions (in µm): *Male holotype*: FWL: 2001, HWL: 1665, F: 441, T: 774, t1: 257, t2: 60, ctt1: 14, Mx4: 116, f1: 410, f2: 249, f3: 182, f4: 153, f5: 96, f6: 108, f7: 95, f8: 92, f9: 101, f10: 80, IO: 372, D: 243, d: 182, IO/D: 1.53, PO: 0.74. *Female allotype*: FWL: 2423, HWL: 1926, F: 537, T: 890, t1: 298, t2: 70, ctt1: 16, Mx4: 113, f1: 421, f2: 268, f3:197, f4: 154, f5: 108, f6: 102, f7: 89, f8: 92, f9: 54, f10: 50, f11: 37, f12: 37, IO: 440, D: 218, d: 134, IO/d: 2.01, PO: 0.61.

Distribution: Southern Western Ghats of Tamil Nadu and Kerala, India between 8.41°N to 9.61°N and 94 m to 994 m. The specimens were collected from green and dry leaves in evergreen forest understorey adjacent to streams.

Type locality: India, Tamil Nadu, Tirunelveli District, Agasthiyamalai Biosphere Reserve, Kalakkad-Mundanthurai Tiger Reserve (KMTR), Ambasamudram Range, Kuthiraivetti.

Remarks: The genus *Phallocaecilius* is recorded for the first time in India. The described new species is widely distributed in the Southern Western Ghats of Tamil Nadu and Kerala. This species is distinguished from the other two species in the genus by the structure of the endophallus and female genitalia. Vaughan *et al.* (1989) discussed the geographic variation of *P. hirsutus*. In *P. indicus* no such variations were found in male or female samples from the different populations studied in the Southern Western Ghats.

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We are grateful to Dr Dhriti Banerjee, Director, Zoological Survey of India, Kolkata for providing necessary facilities and encouragement. We are also grateful to Dr Kazunori Yoshizawa (Hokkaido University, Sapporo, Japan) for valuable taxonomic inputs and critical comments on the manuscript. We extend thanks to Dr P. M. Sureshan, Officer-in-Charge, Western Ghat Regional Centre, Zoological Survey of India, Calicut and Dr Jayasree Thilak and Dr Varadaraju, Southern Regional Centre, Zoological Survey of India, Chennai for providing logistic support for collecting the specimens. We also thank the Principal Chief Conservator of Forests and Chief Wildlife Warden, Tamil Nadu, Chief Conservator of Forests and Field Director, KMTR, Tirunelveli, Wildlife Wardens of Meghamalai Wildlife Sanctuary, Kanyakumari Wildlife Sanctuary, Tamil Nadu and Neyyar Wildlife Sanctuary, Peppara Wildlife Sanctuary and Shendureny Wildlife Sanctuary, Kerala for providing necessary permissions to conduct the study. We also thank Dr Alfonso Neri García Aldrete, Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, México and John Hollier, Muséum d'histoire naturelle, Genève, Switzerland for critical comments.

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A checklist of the parasitic nematodes of freshwater fishes from Argentina

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Abstract: An annotated checklist of the nematodes parasites of Argentinian freshwater fishes is presented. This review includes information for 42 taxa of parasitic nematodes from 56 species of freshwater fish hosts. Fourty nematode species have been reported as adults and two as larvae. Camallanidae was the nematode family with the highest number of taxa (12 species), followed by Cucullanidae (4 species) and Raphidascarididae (4 species and 1 at genus level). The larval nematode *Contracaecum* sp. was the parasite with the widest range of host species, follow by *Spirocamallanus hilarii*, *Spirocamallanus inopinatus,* and *Camallanus corderoi*. Of the 570 species of freshwater fishes reported in Argentina, only 65 (11.4 %) were recorded as hosts of nematodes. Most records were in Characiformes, Siluriformes and Galaxiiformes, which may reflects sampling effort, since its abundance and widely distributions across differents ichthyogeographic provinces of Argentina. Most sampling were done in Great River and Patagonian ichthyogeographic provinces. The small number of examined fish hosts and geographically biased studies may not reflect the real richness and distribution of these parasites. Other obstacles that also contributes to the lack of completeness of this checklist are the problems in the taxonomic validity of some nematode species, doubtful host identification, and poor taxonomic resolution for larval stages of nematodes. Therefore, it is strongly recommended to deposit voucher specimens, including also of the hosts in reference collection, as well as performing integrative studies to elucidate the real taxonomic identity of nematode larvae. This is the first compilation on the nematode parasites of freshwater fishes from Argentina, including three nematode taxa recorded for new host records and four from new localities. Despite this study is exhaustive, the knowledge about parasitic nematodes from Argentinian freshwater fishes is far from complete, since some hydrological basin mainly in Pampean and Andean Cuyan regions and some host families remain unexplored in terms of nematode parasite detection.

Keywords: Nematoda - parasite - freshwater fishes - new hosts - new geographical localities - Neotropical region.

INTRODUCTION

The class Nematoda represents a taxonomical, ecological and geographically diverse helminth assemblage (Luque *et al*., 2011). To date, nematode biodiversity (parasitic and free living forms) has been estimated at 25 043 species, thus representing the fourth species-rich taxa within the kingdom Animalia (Zhang, 2013). Nematodes represent a conspicuous component of the parasite assemblages in fishes and have a considerable importance from veterinary medicine and public health points of view (Moravec, 1998; Luque *et al.,* 2011). According to Luque *et al*. (2016), nematodes are the fourth taxon in terms of species reported in fishes from Southamerica, after Monogenea, Trematoda, and Cestoda.

Research on freshwater fish nematodes from Argentina date back to mid 20th Century. The first publication was by Shuurmans-Stekhoven (1951), who reported larvae of *Contracaecum* sp. in *Pseudoplatystoma corruscans* (Spix & Agassiz) (= *Platystoma* sp.) in the Paraná River, Corrientes Province. Subsequently, Zeiss & Seigneur (1981) reported *Contracaecum rudolphii* Hartwich, 1964 in *Pimelodus albicans* (Valenciennes) and *Salminus brasiliensis* (Cuvier) from Los Quirogas Dam, Santiago del Estero Province. Later Hamann (1982a, b, c, 1984, 1985, 1986, 1995/1996) performed several taxonomic studies about nematode parasites of freshwater fishes from Paraná River basin, contributing to knowledge about the parasitic nematodes of Argentinian freshwater

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fishes. From 1995 to today, the number of descriptions and/or reports have considerably increased (e.g., Ramallo & Torres 1995; Ramallo, 1997, 1999, 2008, 2011, 2012; Brugni & Viozzi, 1999, 2003, 2010; Ailán-Choke *et al.,* 2014, 2017, 2018). Chemes & Takemoto (2011) published a commented list of helminth parasites of freshwater fishes from Middle Paraná System, and Rauque *et al.* (2018) included records of nematode parasites in a study about helminth parasites of alien freshwater fishes in Patagonia. However, an actualized checklist about nematode parasites of Argentinian freshwater fish has not yet been published. Therefore, the knowledge about the nematode parasites of Argentinian freshwater fishes is scattered and the studies are focused mainly on taxonomy.

The aim of this study is to update the list of nematode parasites of freshwater fishes from Argentina. It is based on the compilation of published papers and reports of species herein cited for the first time.

MATERIAL AND METHODS

We compiled and reviewed all publications refering to nematode parasites of Argentinean freshwater fishes (estuarine excluded), during 1951-2021. The bibliographic search was complemented by the information gathered from Host-Parasite Database of the Natural History Museum, London (Gibson *et al.,* 2005), Google Scholar, ScienceDirect and Web of Knowledge. We used the following keywords: Biodiversity, nematodes, parasites, freshwater fishes, Argentina, Parana River basin, Juramento River basin, Bermejo River basin, Colorado River, and Patagonia. Each taxonomic category of Nematoda is presented in alphabetical order, each one followed by author and publication year, and synonyms under which the original records appeared. The list also includes host(s) and localities in which the nematode species was collected (Lo), the geographical coordinates indicated in the publications, the site of infection (SI); the institution where the material is deposited and the accession numbers (MD); developmental stage (DS), references and remarks (when justified).

The taxonomy of nematodes follows Moravec (1998), Anderson *et al.* (2009), and Ailán-Choke & Pereira (2021) for camallanids. Collection acronyms, whenever possible, are as follows: In Argentina: CH-N-FML: Colección de Invertebrados (Sección Helmintos y Anélidos), Fundación Miguel Lillo, San Miguel de Tucumán; CECOAL: Centro de Ecología Aplicada, Corrientes, UNSa-IEBI-I: Colección de Invertebrados del Instituto para el Estudio de la Biodiversidad de Invertebrados, Universidad Nacional de Salta, Salta; CHMLP: Colección de Helmintología del Museo de La Plata, La Plata; MACN-Pa: Colección Nacional de Parasitología, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; UNCo-Pa: Colección Parasitológica de la Universidad Nacional del Comahue, Bariloche; Colección del Museo Provincial de Ciencias Naturales Florentino Ameghino, Santa Fé, Argentina. In other countries: USNPC: U.S. National Parasite Collection, Beltsville, Maryland; IPCAS Helm.: Helminthology Collection, Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice; NHM: The Natural History Museum, London; CHIOC: Helminthological Collection of the Instituto Oswaldo Cruz, Rio de Janeiro, Brazil; IPUAT: Instituto de Parasitología de la Universidad Austral de Chile.

The fish taxonomy follows Mirande & Koerber (2015), Lucena & Gouvea Soares (2016), Mirande & Koerber (2020), Terán *et al.* (2020), Fricke *et al.* (2021), and Froese & Pauly (2021). The names of ichthyogeographic provinces follow López *et al.* (2008). Type material is indicated with H (Holotype), A (Allotype), and P (Paratype) after the collection acronym. The following abbreviations and symbols are used: *new host record by the present authors, **new locality record by the present authors, ● indicates doubtful fish host; ◦ indicates doubtful record of parasite.

RESULTS

The parasite-host list comprises records of 42 taxa of nematode parasites (36 nominal species and 6 identified at generic level), belonging to 3 orders and 12 families. These parasites were associated with 56 species of freshwater fishes from 9 orders and 21 families (Table 1). Fourty nematode taxa were reported as adults and two unidentified species as larvae (*Contracaecum* sp. and *Eustrongylides* sp.). In the particular case of *Hysterothylacium* sp., it was recorded as larvae only in *Odontesthes bonariensis* (Valenciennes), while in the other fish hosts [*Odontesthes hatcheri* (Eigenmann) and *Percichthys trucha* (Valenciennes)] was recorded as adult. Camallanidae was the family with the highest number of species recorded (12), followed by Cucullanidae (4) and Raphidascarididae (4), whereas Guyanemidae and Philometridae are only represented by one species each. The larval nematode *Contracaecum* sp. was the parasite with the widest range of host species, parasitizing 28 fish species, follow by *Spirocamallanus hilarii* Vaz & Pereira, 1934 reported in 15 fish species, *S. inopinatus* Travassos, Artigas & Pereira, 1928 and *Camallanus corderoi* Torres, Teuber & Miranda, 1990; both in 10 fish species (see Table 1). Additionally, we reported new hosts for three taxa [*Spirocamallanus hilarii*, *Rhabdochona acuminata* (Molin, 1860) and *Contracaecum* sp.] and four nematodes were recorded in new localities [*Cucullanus* (*Cucullanus*) *pinnai pinnai* Travassos, Artigas & Pereira, 1928, *Spirocamallanus hilarii*, *Rhabdochona acuminata* and *Contracaecum* sp. in the present survey (see the Parasite-Host list)].

Fish orders with the highest number of nematode

Table 1. List of the Argentinian fish hosts and their nematodes (host species are presented by order and families in alphabetical order). * Doubtful identification of host species. ◦ Doubtful identification of nematode.

Orders	Families	Hosts	Nematodes
Atheriniformes	Atherinopsidae	*Odontesthes bonariensis*	*Camallanus corderoi* *Contracaecum* sp. *Goezia* sp. ◦
		Odontesthes hatcheri (syn. *Patagonina hatcheri*)	*Camallanus corderoi* *Contracaecum* sp. *Hysterothylacium* sp. *Hysterothylacium patagonense* *Rhabdochona* sp. *Rhabdochona acuminata*
Characiformes	Anostomidae	*Megaleporinus obtusidens* (syn. *Leporinus obtusidens*)	*Spinitectus asperus* *Spirocamallanus hilarii* *Spirocamallanus inopinatus*
		Leporinus maculatus *	*Spirocamallanus inopinatus*
	Bryconidae	*Brycon orbignyanus*	*Spirocamallanus inopinatus*
		Salminus brasiliensis	*Contracaecum* sp. *Contracaecum rudolphii* ◦ *Neocucullanus marcelae* *Spirocamallanus hilarii*
	Characidae	*Astyanax abramis*	*Spirocamallanus hilarii*
		Astyanax bimaculatus *	*Spirocamallanus hilarii* *Contracaecum* sp. *Rhabdochona acuminata*
		Bryconamericus iheringi	*Rhabdochona fabianae*
		Piabina thomasi (syn. *Bryconamericus thomasi*)	*Contracaecum* sp. *Spirocamallanus hilarii*
		Oligosarcus jenynsii	*Contracaecum* sp. *Hedruris bifida* *Spirocamallanus hilarii*
		Poptella paraguayensis (syn. *Ephippicharax orbicularis paraguayensis*)	*Spirocamallanus inopinatus*
		Psalidodon anisitsi (syn. *Hyphessobrycon anisitsi*)	*Spirocamallanus hilarii*
		Psalidodon eigenmanniorum (syn. *Astyanax eigenmanniorum*)	*Contracaecum* sp. *Spirocamallanus hilarii*
		Psalidodon endy (syn. *Astyanax endy*)	*Contracaecum* sp. *Spirocamallanus hilarii*
		Psalidodon rutilus (syn. *Astyanax fasciatus*)	*Spirocamallanus hilarii*
	Erythrinidae	*Hoplias argentinensis*	*Contracaecum* sp.
		Hoplias misionera	*Contracaecum* sp. *Spirocamallanus hilarii* *Spirocamallanus inopinatus* *Spirocamallanus tomsici*
	Gasteropelecidae	*Thoracocharax stellatus*	*Procamallanus* (*Denticamallanus*) *ana*
	Prochilodontidae	*Prochilodus lineatus* (syn. *P. platensis*)	*Spinitectus asperus*
	Serrasalmidae	*Piaractus mesopotamicus* (syn. *Colossoma mitrei*)	*Rondonia rondoni* *Spectatus spectatus*
		Serrasalmus marginatus	*Spirocamallanus inopinatus*
		Serrasalmus spilopleura *	*Contracaecum* sp. *Spirocamallanus inopinatus*
		Pygocentrus nattereri (syn. *Serrasalmus nattereri*)	*Contracaecum* sp. *Spirocamallanus inopinatus* *Spirocamallanus tomsici*

Orders	Families	Hosts	Nematodes
Cypriniformes	Cyprinidae	*Cyprinus carpio*	*Contracaecum* sp.
Cyprinodontiformes	Anablepidae	*Jenynsia alternimaculata*	*Contracaecum* sp. *Cucullanus* (*Cucullanus*) *pinnai pinnai* *Spirocamallanus hilarii* *Rhabdochona acuminata*
		Lebias multidentata (syn. *Jenynsia multidentata)*	*Rhabdochona acuminata* *Camallanus corderoi*
		Jenynsia obscura	*Contracaecum* sp.
Galaxiiformes	Galaxiidae	*Galaxias maculatus*	*Camallanus corderoi* *Contracaecum sp.* *Eustrongylides* sp. *Eustrongylides tubifex* *Hedruris* sp. *Hedruris suttonae* *Hysterothylacium patagonense* *Placonema pataguense* *Rhabdochona acuminata*
		Galaxias platei	*Ascarophis patagonica* *Camallanus corderoi* *Contracaecum sp.* *Hedruris* sp. *Hedruris suttonae* *Rhabdochona* sp. *Rhabdochona acuminata*
Centrarchiformes	Percichthyidae	*Percichthys colhuapiensis*	*Camallanus tridentatus* ◦
		Percichthys trucha	*Camallanus corderoi* *Camallanus tridentatus* ◦ *Contracaecum* sp. *Hedruris* sp. *Hysterothylacium* sp. *Hysterothylacium patagonense* *Philonema percichthydis* *Pseudodelphis limnicola* *Rhabdochona* sp. *Rhabdochona acuminata*
Perciformes	Sciaenidae	*Pogonias cromis*	*Dichelyne* (*Cucullanellus*) *mariajuliae*
Salmoniformes	Salmonidae	*Oncorhynchus mikiss*	*Camallanus corderoi* *Camallanus tridentatus* ◦ *Contracaecum* sp. *Goezia* sp. ◦ *Hedruris* sp. *Hedruris suttonae* *Rhabdochona* sp. *Rhabdochona acuminata* *Hysterosthylacium patagonense*
		Salmo trutta	*Camallanus corderoi* *Contracaecum* sp. *Hedruris* sp. *Hedruris suttonae* *Hysterosthylacium patagonense*
		Salmo salar	*Camallanus corderoi* *Contracaecum* sp.
		Salvelinus fontinalis	*Camallanus tridentatus* ◦ *Camallanus corderoi* *Contracaecum* sp. *Hedruris suttonae* *Hysterosthylacium patagonense*

Orders	Families	Hosts	Nematodes
Siluriformes	Diplomystidae	*Olivaichthys viedmensis*	*Contracaecum* sp.
		Olivaichthys mesembrinus (syn. *Diplomystes mesembrinus*)	*Rhabdochona acuminata*
	Callichthyidae	*Corydoras paleatus*	*Spirocamallanus pintoi*
		Corydoras micracanthus	*Spirocamallanus pintoi*
	Doradidae	*Pterodoras granulosus*	*Klossinemella iheringi* *Rondonia rondoni* *Spectatus spectatus*
	Heptapteridae	*Heptapterus mustelinus*	*Cucullanus* (*Cucullanus*) *pinnai pinnai*
		Pimelodella gracilis	*Spirocamallanus juana*
		Rhamdia quelen	*Contracaecum* sp.
		Rhamdia sapo	*Hysterothylacium rhamdiae*
	Loricariidae	*Rineloricaria steinbachi* (syn. *Loricaria steinbachi*)	*Raphidascaris* (*Sprentascaris*) *saltaensis*
		Hypostomus cordovae	*Raphidascaris* (*Sprentascaris*) *marano*
	Pimelodidae	*Luciopimelodus pati*	*Cucullanus* (*Cucullanus*) *pinnai pinnai* *Spirocamallanus inopinatus*
		Pimelodus albicans	*Contracaecum* sp. *Contracaecum rudolphii* ◦ *Cucullanus* (*Cucullanus*) *pinnai pinnai* *Spinitectus asperus* *Spirocamallanus hilarii* *Spirocamallanus juana* *Spirocamallanus rarus* *Spirocamallanus tomsici*
		Pimelodus maculates (syn. *Pimelodus clarias maculatus)*	*Cucullanus* (*Cucullanus*) *pinnai pinnai* *Spirocamallanus inopinatus* *Spirocamallanus neocaballeroi* *Spirocamallanus pimelodus*
		Pseudoplatystoma corruscans	*Contracaecum* sp. *Cucullanus* (*Cucullanus*) *pinnai pinnai* *Goezia spinulosa* *Spirocamallanus inopinatus*
		Sorubim lima	*Contracaecum* sp.
		Zungaro zungaro (syn. *Paulicea luetkeni*)*	*Cucullanus paulicea*
	Trichomycteridae	*Hatcheria macraei* (syn. *Thrichomycterus macraei*)	*Rhabdochona acuminata*
		Trichomycterus corduvensis	*Spirocamallanus huacraensis*
		Trichomycterus spegazzinii	*Contracaecum* sp. *Cucullanus* (*Cucullanus*) *pinnai pinnai* *Spirocamallanus hilarii* *Spirocamallanus huacraensis* *Spirocamallanus pintoi* *Rhabdochona acuminata*

taxa were Siluriformes (32), Characiformes (24), and Galaxiiformes (11). Among Siluriformes, pimelodids present the highest number of nematode taxa recorded, *Pimelodus albicans* (Valenciennes) with eight taxa recorded, followed by *P. maculatus* Lacépède, and *Pseudoplatystoma corruscans* (Spix & Agassiz) (four each) (see Table 1). *Trichomycterus spegazzini* (Berg) (Siluriformes) has six nematode taxa recorded. Among Galaxiiformes, *Galaxias maculatus* (Jenyns) with nine taxa and *G. platei* Steindachner with eight taxa (see Table 1). In the case of Characiformes, the bryconid *Salminus brasiliensis* presents four taxa, the characids *Astyanax lacustris* (Luetken) and *Oligosarcus jenynsii* (Günther) has three taxa each one.

Most records of nematode parasite in freshwater fishes were from Great River ichthyogeographic province, especially in Salta and Corrientes provinces with 35 and 23 records of host-nematode parasite associations, respectively; and Patagonian ichthyogeographic provinces, represented mainly by studies carried out in Río Negro province with 36 records of host-nematode parasite associations. The remaining ichthyological provinces present few records or none like in the Andean-Cuyan region.

PARASITE-HOST LIST

Class Nematoda
Subclass Adenophorea
Order Enoplida
Superfamily Dioctophymatoidea
Family Dioctophymatidae
Genus *Eustrongylides* Jagerskiöld, 1909
***Eustrongylides* sp.**

Host *Galaxias maculatus* (Jenyns)
SI: Caudal peduncle. Lo: Gutierrez Lake (41°12'S, 71°26'W) (Brugni & Viozzi, 1999) and (41°10'S, 71°24'W) (Guagliardo *et al.,* 2019), Moreno Lake (41°04'S, 71°33'W) and Quillén Lake (39°25'S, 71°20'W) (Brugni & Viozzi, 2003), all Río Negro Province. MD: Not indicated. DS: Third and four-stage larvae were found inside melanized capsules. Remark: The larvae have always been found in conspicuous, external, and strongly melanized cysts on the caudal peduncle of *G. maculatus* (Brugni & Viozzi, 1999, 2003). Moravec (1998) mentioned that the species identification of *Eustrongylides* larvae is problematic and that the only reliable way to determine the species is to obtain adult nematodes from experimental infections to the definitive host (piscivorous bird).

***Eustrongylides tubifex* (Nitzsch, 1819)**

Host *Galaxias maculatus* (Jenyns)
SI: Caudal peduncle. Lo: Moreno Lake and Quillén Lake, Río Negro Province. MD: Not reported. DS: Third stage larvae inside melanized capsules. Reference: Brugni & Viozzi (2003). SI: Caudal peduncle. Lo: Carilafquén, Neuquén Province. MD: MACN-Pa # 467 DS: Larvae. Reference: Viozzi *et al.* (2009).

Subclass Secernentea
Order Ascaridida
Superfamily Ascaridoidea
Family Anisakidae
Genus *Contracaecum* Railliet & Henry, 1912

Synonyms: *Kathleena* Leiper & Atkinson, 1914; *Amphicaecum* Walton, 1927; *Cerascaris* Cobb, 1929; *Contracaecum* (*Ornitocaecum*) Mozgovoi, 1951; *Contracaecum* (*Synthetonema*) Kreis, 1952.

***Contracaecum* sp.**

Host *Astyanax lacustris* (Luetken)
SI: Corporal cavity. Lo: El Tunal Reservoir (25°15'S, 64°25'W), Salta Province. MD: Not indicated. DS: Larvae. Reference: Cancino & Ramallo (2008). SI: Corporal cavity. Lo: Itaú River (22°20'S, 64°05'W), Salta Province. MD: CH-N-FML# 7481. DS: Larvae. Reference: Antelo *et al.* (2016).

Host *Cyprinus carpio* Linnaeus
SI: corporal cavity. Lo: Casa de Piedra Reservoir (38°10'S, 67°09'W) and downstream Ballester Dam (38°43.9'S, 68°10'W), Colorado River; Herradura Backwater (38°57.44'S, 68°10.5'W); China Muerta Town (38°59.5'S, 68°19'W) and downstream Arroyito Dam (39°04.5'S, 68°33'W), Limay River; Allen City (39°02'S, 67°50'W) and Guardia Mitre Town (40°26.5'S, 63°41'W), Negro River; all Río Negro Province. MD: not indicated. DS: Larvae. Reference: Rauque *et al.* (2018). SI: Liver and visceral fat. Lo: Ingeniero Ballester dam (38°43'S, 68°10'W), Río Negro Province. MD: MACN-Pa # 562/1. DS: Larvae. Reference: Waicheim *et al.* (2014).

Host *Galaxias maculatus* (Jenyns)
SI: Corporal cavity, gonads. Lo: Moreno (41°05'S, 71°35'W) and Escondido (39°09'S, 71°17'W) Lakes, Río Negro Province. MD: Not indicated. DS: Larvae. Reference: Ortubay *et al.* (1994). SI: Abdominal cavity. Lo: Lakes Ñorquinco (39°09'S, 71°17'W); Quillén (39°25'S, 71°20'W); Huechulafquén (39°45'S; 71°25'W); Lácar (40°10'S; 71°30'W); Machónico (40°20'S, 71°33'W); Meliquina (40°23'S, 71°17'W); Filo Hua Hum (40°30'S, 71°17'W); Villarino (40°28'S, 71°35'W), Espejo Chico (40°35'S, 71°44'W); Traful (40°37'S, 71°25'W); Bailey Willis (40°38'S, 71°40'W); Espejo (40°41'S, 71°40'W) Correntoso (40°44'S, 71°39'W); Patagua (40°47'S, 71°37'W); Verde (40°46'S, 71°39'W); Nahuel Huapi (40°48'S, 71°39'W); El Trébol (41°04'S, 71°30'W); Morenito (41°05'S, 71°31'W); Escondido (41°05'S,

71°35'W); Mallín Ingeniero (41°15'S, 71°40'W); Llum (41°16'S, 71°40'W); Mascardi (41°17'S, 71°38'W); Fonck (41°18'S, 71°43'W); Hess (41°22'S, 71°43'W), Los Césares (41°19'S, 71°43'W); Verde (Villa Mascardi) (41°20'S, 71°31'W); Roca (41°21'S, 71°25'W); Los Moscos (41°21'S, 71°36'W); Juventus (41°22'S, 71°31'W); Huala Hue (41°25'S, 71°30'W); Steffen (41°31'S, 71°33'W); Rivers: Caleufu (40°30'S, 71°17'W), Ñirihuau (41°06'S, 71°10'W), Santa Cruz (50°00'S, 69°00'W), and Senillosa Channel (Limay River) (38°50'S, 68°30'W), Lakes. Patagonia. MD: MACN-Pa 464. DS: Larvae. References: Viozzi *et al.* (2009); Fernandez *et al.* (2015).

Host *Galaxias platei*
SI: Liver. Lo: Rosario Lake (43°15'S, 71°30'W), Chubut Province and Pueyrredón Lake (47°16'S, 72°00'W), Santa Cruz Province. MD: Not indicated. DS: Larvae. Reference: Ortubay *et al.* (1994).

Host *Hoplias argentinensis* Rosso *et al.*
SI: Free or encapsulated in abdominal cavity. Lo: Lago 2 (34°02'S, 59°07'W), Buenos Aires Province; Lagoon 2 (34°46'S, 63°38'W) and Lagoon 8 (33°06'S, 63°03'W) Córdoba Province. MD: Not indicated. DS: Third-stage larvae (Type 2). Reference: Mancini *et al.* (2014).

Host *Hoplias misionera* Rosso *et al.*
SI: Free or encapsulated in abdominal cavity, mesenteries. Lo: Pilcomayo River (22°22'S, 62°32'W), Salta Province. MD: CH-N-FML# 7771. DS: Larvae. Reference: Ramallo *et al.* (2020).

Host *Jenynsia alternimaculata* (Fowler) **
SI: Abdominal cavity, mesenteries. Lo: Isasmendi Stream (24°48'S, 65°26'W) and Stream afluent to Yacones River (24°31'S, 65°24'W), Salta Province. MD: CH-N-FML # 7514. DS: Larvae. Reference: Ailán-Choke *et al.* (2014). SI: abdominal cavity, mesenteries. Lo: Yacones River (24°40'S, 65°24'W) and Arias-Arenales River (24°48'S, 65°25'W), Salta Province. MD: UNSa-IEBI-I # 055. DS: Larvae. Reference: Present study. Remarks: New locality records.

Host *Jenynsia obscura* (Weyenbergh)
SI: Abdominal cavity. Lo: Vis-Vis River (27°15'S, 66°35'W) and Agua Fresca Dam (27°16'S, 66°35'W), Catamarca Province. MD: CH-N-FML # 07479. DS: Larvae. Reference: Ramallo & Padilla Bortayro (2011).

Host *Odontesthes bonariensis* (Valenciennes)
SI: Corporal cavity. Lo: lagoon south of the Córdoba Province (34°36'S, 64°24'W). MD: Not indicated. DS: Larvae. Reference: Mancini *et al.* (2005). SI: Corporal cavity. Lo: Shallow lake, Córdoba Province. MD: Not indicated. DS: Larvae. Reference: Mancini *et al.* (2006). SI: Corporal cavity. Lo: La Viña Reservoir, (31°17'S, 65°01'W), Córdoba Province. MD: Not indicated. DS: Larvae. Reference: Mancini *et al.* (2008). SI: Mesentery. Lo: Salada Grande, General Lavalle (36°55'S, 56°58'W) and Lacombe, Lezama (35°49'S, 57°49'W) lagoons, Buenos Aires Province. MD: CHMLP. DS: Larvae (L3). Reference: Drago (2012). SI: Free or encapsulated in abdominal cavity. Lo: Reservoir 3 (31°17'S, 65°01'W), Lake 1 (33°00'S, 63°55'W), Lagoon 3 (33°48'S, 64°51'W), Lagoon 5 (33°30'S, 63°06'W), Lagoon 6 (34°28'S, 64°23'W), Lagoon 7 (33°25'S, 62°53'W), Córdoba Province. MD: Not indicated. DS: Third-stage larvae (Type 2). Reference: Mancini *et al.* (2014). SI: Free or encapsulated in abdominal cavity. Lo: Reservoir 6 (32°48'S, 65°28'W), Lagoon 1 (33°59'S, 65°24'W), San Luis Province. MD: Not indicated. DS: Third-stage larvae (Type 2). Reference: Mancini *et al.* (2014). SI: Abdominal cavity. Lo: La Plata River (34°28'S, 58°23'W); Lacombe Pampaen Lake (35°49'S, 57°53'W); Chascomús pampean Lake (35°37'S, 58°00'W) Buenos Aires Province. MD: CHMLP. DS: Third-stage larvae. Reference: Flores *et al.* (2016). SI: Abdominal cavity. Lo: Casa de Piedra Reservoir (38°10'S, 67°09'W), Colorado River, La Pampa-Río Negro Provinces and Pellegrini Lake (38°41'S, 68°00'W), Neuquén River, Río Negro Province. MD: MACN-Pa. DS: Larvae. Reference: Rauque *et al.* (2018).

Host *Odontesthes hatcheri* (Eigenmann) (syn. *Patagonina hatcheri*)
SI: Intestine. Lo: Moreno Lake (41°06'S, 71°32'W), Río Negro Province; Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces. MD: Not indicated DS: Adults and larvae. Reference: Ortubay *et al.* (1994). SI: Intestine wall. Lo: El Chañar (Neuquén River) (38°34'S, 68°24'W), Caleufú River (Limay River) (40°23'S, 70°44'W), Neuquén Province; Carrilafquén Chica Lagoon (41°12'S, 69°25'W); Morenito lake (41°02'S, 68°34'W); Moreno Oeste Lake (41°06'S, 71°32'W), Río Negro Province; Musters (45°25'S, 69°11'W), Chubut Province. MD: CHMLP. DS: Third- stage larvae. Reference: Flores *et al.* (2016).

Host *Oligosarcus jenynsii* (Günther)
SI: Free or encapsulated in abdominal cavity. Lo: Lagoon 2 (34°46'S, 63°38'W), Lagoon 4 (33°09'S, 63°31'W), Lagoon 9 (34°53'S, 63°31'W), Córdoba Province. MD: Not indicated. DS: Third- stage larvae (Type 2). Reference: Mancini *et al.* (2014). SI: Free or encapsulated in abdominal cavity. Lo: Stream (33°45'S, 69°02'W) Mendoza Province. MD: Not indicated. DS: Third- stage larvae (Type 2). Reference: Mancini *et al.* (2014).

Host *Olivaitchthys viedmensis* (MacDonagh)
SI: Mesentery, stomach, intestine. Lo: Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces. MD: Not indicated. DS: Larvae. Reference: Ortubay *et al.* (1994).

Host *Oncorhynchus mykiss* (Walbaum)
SI: Corporal cavity. Lo: El Chañar Reservoir (38°34'S, 68°24'W) Neuquén River; Arroyito Reservoir (38°40'S, 68°33´W), Limay River; Ballester Dam (38°43'S, 68°10'W), Neuquén River; Ramos Mexia Reservoir (39°26'S, 68°56'W), Limay River; Piedra del Aguila Reservoir (40°19'S, 70°93'W), Limay River; Nahuel Huapi Lake (41°04'S, 71°25'W), Limay River; Moreno Lake (41°04'S, 71°33'W), Limay River, Escondido Lake (41°05'S, 71°35'W), Limay River, Río Negro Province; Traful Lake (40°38'S, 71°24'W), Limay River; Alicurá Reservoir (40°40'S, 71°00'W), Limay River, Neuquén Province; Cholila Lake (42°27'S, 71°40'W), Futaleufú River, Chubut Province. MD: MACN–Pa. DS: Larvae. Reference: Rauque *et al.* (2018).

Host *Percichthys trucha* (Valenciennes)
SI: Intestine. Lo: Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces; Moreno Lake (Río Limay) (41°04'S, 71°33'W), and Escondido Lake (41°05'S, 71°35'W), Río Negro Province. MD: Not indicated. DS: Larvae. Reference: Ortubay *et al.* (1994).

Host *Piabina thomasi* (Fowler) (syn. *Bryconamericus thomasi*) **
SI: Abdominal cavity, mesenteries. Lo: Puerta de Díaz Dam (25°16'S, 65°31'W), Salta Province. MD: UNSa-IEBI-I # 145/1. DS: Larvae. Reference: Párraga & Davies (2015). SI: Abdominal cavity, mesenteries. Lo: Puerta de Díaz Dam (25°16'S, 65°31'W), Salta Province. MD: UNSa-IEBI-I # 0055. DS: Larvae. Reference: Present study. Remarks: New locality record.

Host *Pimelodus albicans* (Valenciennes)
SI: Free or encapsulated in abdominal cavity. Lo: Laguna 2 (35°46'S, 63°38'W), Laguna 7 (33°25'S, 62°53'W), Río Cuarto (33°09'S, 64°16'W), Córdoba Province. MD: Not indicated. DS: Third stage larvae (Type 2). Reference: Mancini *et al.* (2014). SI: Free or encapsulated in abdominal cavity, mesenteries, intestine or liver Lo: Misión La Paz, Pilcomayo River (22°22'S, 62°32'W), Rivadavia Department, Salta Province. MD: CH-N-FML#7772. DS: Third stage larvae (Type 2). Reference: Ramallo *et al*. (2020).

Host *Psalidodon eigenmanniorum* (Cope) (syn. *Astyanax eigenmanniorum*)
SI: Free or encapsulated in abdominal cavity. Lo: Castaño River, San Juan Province. MD: CH-N-FML #07799. DS: Larvae. Reference: Ramallo & Cancino (2021).

Host *Psalidodon endy* (Mirande, Aguilera & Azpelicueta) (syn. *Astyanax endy*) ***
SI: Abdominal cavity, mesenteries. Lo: Campo Alegre Dam (24°34'S, 65°21'W), Salta Province. MD: UNSa-IEBI-I # 0055. DS: Larvae. Reference: Present study. Remarks: New host and locality records.

Host *Pseudoplatystoma corruscans* (Spix & Agassiz)
SI: Stomach and intestine. Lo: Parana River, Santa Fé Province. MD: CH-N-FML# 212 (missing material). DS: Larvae. Reference: Schuurmans Stekhoven (1951). SI: Free or encapsulated in abdominal cavity, mesenteries. Lo: Pilcomayo River (22°22'S, 62°32'W), Salta Province. MD: CH-N-FML #7769. DS: Larvae. Reference: Ramallo *et al.* (2020).

Host *Pygocentrus nattereri* Kner
SI: Free or encapsulated in abdominal cavity, mesenteries. Lo: Pilcomayo River (22°22'S, 62°32'W) Salta Province. MD: CH-N-FML# 7785. DS: Larvae. Reference: Ramallo *et al.* (2020).

Host *Rhamdia quelen* (Quoy & Gaimard)**
SI: Free or encapsulated in abdominal cavity. Lo: Lake 2, Buenos Aires (34°03'S, 59°07'W), Buenos Aires Province. MD: Not indicated. DS: Third-stage larvae (Type 2). Reference: Mancini *et al.* (2014). SI: Free or encapsulated in abdominal cavity. Laguna 2 (36°46'S, 63°38'W), Lagoon 9 (34°53'S, 63°31'W), Córdoba Province. MD: Not indicated. DS: Third-stage larvae (Type 2). Reference: Mancini *et al.* (2014). SI: Free or encapsulated in abdominal cavity. Lo: El Cero Dam, Figueroa Water System (27°07'S, 63°37'W), Santiago del Estero Province. MD: CH-N-FML # 07787. DS: Third stage larvae (Type 2). Reference: Present study. Remarks: New locality record.

Host *Salminus brasiliensis* (Cuvier)
SI: Intestinal caecum and peritoneum of intestine. Lo: Río Hondo Reservoir (27°31'S, 64°53'W) Tucumán-Santiago del Estero Provinces. MD: CH-FML # 01830 and IPUAT # 0247. DS: Larvae. Reference: Ramallo & Torres (1995).

Host *Salmo salar* Linnaeus
SI: Mesentery, stomach and intestine. Lo: Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces. MD: Not indicated. DS: Larvae. Reference: Ortubay *et al.* (1994). SI: Abdominal cavity. Lo: Piedra del Águila Reservoir (40°19'S, 70°03'W), Limay River, Río Negro-Neuquen Provinces. MD: MD: MACN-Pa. DS: Larvae. Reference: Rauque *et al.* (2018).

Host *Salmo trutta* Linnaeus
SI: Corporal cavity. Lo: Pichi Picún Leufú Reservoir (40°01'S, 70°00'W); Piedra del Águila Reservoir (40°19'S, 70°03'W); Alicurá Reservoir (40°35'S, 70°50'W); Nahuel Huapi Lake (41°05'S, 71°25'W); Moreno Lake (41°04'S, 71°33'W), all Limay River, Río Negro Province. MD: MACN-Pa. DS: Larvae. Reference: Rauque *et al.* (2018).

Host *Salvelinus fontinalis* (Mitchill)
SI: Corporal cavity. Lo: Moreno Lake (41°05′S 71°30′W),

Limay River, Neuquén Province. MD: MACN-Pa. DS: Larvae. Reference: Rauque *et al*. (2018).

Host *Serrasalmus spilopleura* Kner •
SI: Encysted in mesentery, wall of intestine, stomach and pyloric caecum. Lo: Riachuelo basin, Paraná River, Corrientes Province. MD: Not indicated. DS: Larvae. Reference: Hamann (1995/1996, 1999). Remarks: According to Mirande & Koerber (2020), *S. spilopleura* is not distributed in Argentina, but this record could correspond to *Serrasalmus maculatus* Kner (Jégu & Santos, 2001; Mirande & Koerber, 2020).

Host *Sorubim lima* (Bloch & Schneider)
SI: Free or encapsulated in abdominal cavity, mesenteries. Lo: Pilcomayo River (22°22'S, 62°32'W), Salta Province. MD: CH-N-FML# 2767. DS: Larvae. Reference: Ramallo *et al*. (2020).

Host *Trychomycterus spegazzinii* (Berg)
SI: Abdominal cavity, mesenteries. Lo: Stream afluent to Yacones River (24°31'S, 65°24'W), Salta Province. MD: UNSa-IEBI-I #052. DS: Larvae. Reference: Ailán-Choke *et al.* (2014).

Contracaecum jorgei Sardella, Mancini, Salinas, Simões & Luque, 2020

Host *Hoplias argentinensis* Rosso *et al*.
SI: Intestine. Lo: Pampean shallow lakes (33°25'S, 62°54'W), Unión Department, Córdoba Province. MD: (P) CHIOC # 38926. DS: Third stage larvae larvae. Reference: Sardella *et al.* (2020). Remarks: *Contracaecum jorgei* was morphologically described for adults and fourth-stage larvae (L4) found in the bird *Nannopterum brasilianus* and third-stage larvae (L3) found in *H. argentinensis*. Additionally, in the molecular analyses, sequences obtained from adult, L4 and L3 specimens of this parasite were similar and grouped, forming an independent lineage (Sardella *et al*., 2020).

Contracaecum rudolphii Hartwich, 1964

Synonyms: *Contracaecum spiculigerum* (Rudolphi, 1809)*; Ascaris siluriglanidis* Linstow, 1883.
Host *Pimelodus albicans* (Valenciennes) ◦
SI: Mesentery. Lo: Los Quirogas Dam (27°41'S, 64°18'W), Santiago del Estero Province. MD: Not indicated. DS: Larvae. Reference: Zeiss & Seigneur (1981).

Host *Salminus brasiliensis* (Cuvier) ◦
SI mesentery. Lo: Los Quirogas Dam (27°41'S, 64°18'W), Santiago del Estero Province. MD: Not indicated. DS: Larvae. Reference: Zeiss & Seigneur (1981). SI: Intestinal caecum and peritoneum of intestine. Lo: Río Hondo Reservoir (27°31'S, 64°53'W) Tucumán-Santiago del Estero Provinces. MD: CH-N-FML # 01830 and IPUAT # 0247. DS: Larvae. Reference: Ramallo & Torres (1995). Remarks: Zeiss & Seigneur (1981) also identified adults of *Contracaecum rudolphii* in the ventricle of *Phalacrocorax brasilianus*, but they did not provided morphometric characterizations of the larval stages and adult forms of this parasite. Moreover, the type specimens were not deposited in a collection. Thus, we consider that this record is doubtful and has to be carefully reviewed.

Genus Goezia Zeder, 1800

Synonyms: *Cochlus* Zeder, 1803; *Prionoderma* Rudolphi, 1808; *Lecanocephalus* Diesing, 1839.

Goezia sp.

Host *Odontesthes bonariensis* ◦
SI: Corporal cavity. Lo: Casa de Piedra Reservoir (38°10'S, 67°30'W), Río Negro-La Pampa Provinces. MD: Not indicated. DS: Not indicated. Reference: Gilbert *et al*. (1993), Ortubay *et al.* (1994). Gilbert *et al*. (1993) recorded *Cucullanus* sp. in *O. mykiss* and *O. bonariensis* from Patagonia, but these records belongs to *Goezia* sp. according to Ortubay *et al.* (1994).

Host *Oncorhynchus mykiss* (Walbaum) ◦
SI: Corporal cavity. Lo: Casa de Piedra Reservoir (38°10'S, 67°30'W), Río Negro-La Pampa Provinces. MD: Not indicated. DS: Not indicated. Reference: Gilbert *et al*. (1993), Ortubay *et al*. (1994). Remarks: Gilbert *et al*. (1993) recorded *Cucullanus* sp. in *O. mykiss* and *O. bonariensis* from Patagonia, but these records belongs to *Goezia* sp. according to Ortubay *et al.* (1994). Despite Ortubay *et al.* (1994) did not report the stage of development of this parasite, considering site of infection it can be inferred that it is a larval form in a paratenic host (Rauque *et al.,* 2018). *Odontesthes bonariensis* and *O. mykiss* are introduced species into Patagonia, they are present in in various lakes and rivers of the Andes Mountains (Cussac *et al.,* 2016). Thus, *Goezia* sp. could be considered an introduced parasite with a high specificity for *O. bonariensis* and *O. mykiss* and have not yet switched to the native fish species in Patagonia (Rauque *et al.,* 2018).

Goezia spinulosa (Diesing, 1839)

Host *Pseudoplatystoma corruscans* (Spix & Agassiz)
SI: Stomach. Lo: Río Paraná Medio, Corrientes Province. MD: CECOAL. DS: Adults (males, females). Reference: Hamann (1984).

Family Raphidascarididae
Genus *Hysterothylacium* Ward & Magath, 1916
***Hysterothylacium* sp.**

Host *Odontesthes bonariensis* (Valenciennes)
SI: Mesentery. Lo: Salada Grande, General Lavalle (36°55'S, 56°58'W) and Lacombe, Lezama (35°49'S, 57°49'W) Lagoons, Buenos Aires Province. MD: CHMLP. DS: Larvae (L3). Reference: Drago (2012). Remarks: The life cycles and larval developmental of *Hysterothylacium* species are little known. *Hysterothylacium* larvae occur in Neotropical freshwater fishes serving as paratenic host (Moravec, 1998). Thus, *Odontesthes bonariensis* may be likely paratenic host for this parasite.

Host *Odontesthes hatcheri* (Eigenmann) (syn. *Patagonina hatcheri*)
SI: Intestine. Lo: Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces. MD: Not indicated. DS: Adults. Reference: Ortubay *et al*. (1994). Remarks: *Hysterothylacium* sp. may be a new parasite species or likely, it belongs to *Hysterothylacium patagonense*, which was later record in *Odontesthes hatcheri* by Flores *et al*. (2016).

Host *Percichthys trucha* (Valenciennes)
SI: Intestine. Lo: Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces, Escondido Lake (41°05'S, 71°35'W) and Moreno Lake (41°06'S, 71°32'W), Río Negro Province. MD: Not indicated. DS: Adult. Reference: Ortubay *et al.* (1994).

***Hysterothylacium patagonense* Moravec, Urawa & Coria, 1997**

Host *Percichthys trucha* (Valenciennes)
SI: Intestine (secondarily found in abdominal cavity). Lo: Aluminé Lake (38°55'S, 71°10'W) Negro River drainage system, Neuquen Province. MD: Type-material: IPCAS Helm. (holotype, allotype, and some paratypes, Cat. # 675); NHM (paratypes, Reg. # 1996.5.30-1-5), and Meguro Parasitological Museum, Tokyo (paratypes, Cat. # 19695). DS: Adults and third and fourth stage larvae. Reference: Moravec *et al.* (1997a).

Host *Galaxias maculatus* (Jenyns)
SI: Abdominal cavity. Lo: Quillén Lake, Neuquén; Espejo Chico Lake and Escondido lake, Río Negro Province. MD: MACN-Pa 465. DS: Larvae. Reference: Viozzi *et al*. (2009).

Host *Odontesthes hatcheri* (Eigenmann)
SI: Intestine. Lo: Morenito lake (41°02'S, 68°34'W); Moreno Oeste lake (41°06'S, 71°32'W), Río Negro Province. MD: CHMLP. DS: Fourth stage larvae. Reference: Flores *et al.* (2016).

Host *Oncorhynchus mykiss* (Walbaum)
SI: Intestine. Lo: Lake Alumine (38°55'S, 71°10'W) and Lake Huechulafquen, Negro River drainage system, Neuquen Province. MD: Not indicated. DS: Third- and fourth-stage larvae. Reference: Moravec *et al.* (1997a).

Host *Salvelinus fontinalis* (Mitchill)
SI: Intestine. Lo: Lake Alumine (38°55'S, 71°10'W), Negro River drainage system, Neuquen Province. MD: Not indicated. DS: Third- and fourth-stage larvae. Reference: Moravec *et al.* (1997a).

Host *Salmo trutta* Linnaeus
SI: Intestine. Lo: Lake Huechulafquen, Negro River drainage system, Neuquen Province. MD: Not indicated. DS: Third- and fourth-stage larvae. Reference: Moravec *et al.* (1997a). Remarks: According to Moravec *et al.* (1997a) these third- and fourth-stage larvae, like those found in *O. mykiss* and *S. fontinalis*, are morphologically and biometrically identical with those of *H. patagonense* from the type-host, *Percichthys trucha*. Moreover, since *H. patagonense* seems to be the only *Hysterothylacium* species present in Alumine and Huechulafquen lakes, the larvae were considered to belong to *H. patagonense*. These three salmonid species are introduced into Argentina, so apparently they can adquire infection by feeding on intermediate or paratenic hosts, but the nematode larvae cannot mature in them. Thus, salmonids may be considered paratenic hosts of this nematode species.

***Hysterothylacium rhamdiae* Brizzola & Tanzola, 1995**

Host *Rhamdia sapo* (Valenciennes)
SI: Intestine. Lo: Napostá stream (38°08'S, 61°47'W); and Sauce Grande River (38°43'S, 62°15'W), Buenos Aires Province. MD: Holotype and allotype MACN # 373, and paratypes Laboratorio de Parasitología, Depto. Biología y Bioquímica, Universidad Nacional del Sur # 001-004. DS: Adults (males, females). Reference: Brizzola & Tanzola (1995).

Genus *Raphidascaris* Railliet & Henry, 1915

Synonyms: *Ichthyascaris* Wu, 1949; *Neogoezia* Kreis, 1937; *Sprentascaris* Petter & Cassone, 1984.

Subgenus *Sprentascaris* Petter & Cassone, 1984
***Raphidascaris* (*Sprentascaris*) *marano* Ramallo, 2009**

Host *Hypostomus cordovae* (Günther)
SI: Intestine. Lo: Marapa River (27°37'S, 65°41'W), Tucumán Province. MD: Holotype CH-N-FML # 07462-A; allotype CH-N-FML # 07462-B, and paratypes CH-N-FML # 07463. DS: Adults. Reference: Ramallo (2009).

***Raphidascaris* (*Sprentascaris*) *saltaensis* Ailán Choke, Ramallo & Davies, 2017**

Host *Rineloricaria steinbachii* (Regan) (syn. *Loricaria steinbachii*)
SI: Intestine. Lo: La Caldera River (24°35'S, 65°22'W), Salta Province. MD: Holotype: female CH-N-FML #07663; Allotype: not assigned; Paratypes CH-N-FML # 07665. DS: Adults. Reference: Ailán-Choke *et al*. (2017).

Superfamily Seuratoidea
Family Cucullanidae
Genus *Cucullanus* Müller, 1777
Subgenus *Cucullanus* Müller, 1777
***Cucullanus* (*Cucullanus*) *pauliceae* Vaz & Pereira, 1934**

Host *Zungaro zungaro* (Humboldt) [syn. *Paulicea luetkeni* (Steindachner)] ●
SI: Small and large intestine. Lo: Paraná Medio River, Corrientes Province. MD: CECOAL. DS: Adults. Reference: Hamann (1984). Remarks: Host originally reported as *Paulicea lutkeni* (synonym of *Z. zungaro*). According to Mirande & Koerber (2020), *Z. zungaro* is not distributed in Argentina. Probably, due to similarity among them, the original record of *P. lutkeni* by Hamann (1984) corresponds to *Zungaro jahu*, which inhabit in the Parana River basin.

***Cucullanus* (*Cucullanus*) *pinnai pinnai* Travassos, Artigas & Pereira, 1928**

Host *Heptapterus mustelinus* (Valenciennes)
SI: Stomach. Lo: El Tunal Dam (25°15'S, 64°25'W), Salta Province. MD: Not indicated. DS: Adults. Reference: Cancino & Ramallo (2008).

Host *Jenynsia alternimaculata* (Fowler)
SI: Intestine. Lo: Strem affluent of Yacones River (24°31'S, 65°24'W), Isasmendi Stream (24°48'S, 64°26'W), Salta Province. MD: CH-N-FML # 7512, UNSa-IEBI-I # 050. DS: Adults. Reference: Ailán-Choke *et al.* (2014).

Host *Luciopimelodus pati* (Valenciennes)
SI: Intestine. Lo: Río Paraná Medio, Corrientes Province. MD: Not indicated. DS: Adults and third- and fourth-stage larvae. Reference: Hamann (1985).

Host *Pimelodus maculatus* Lacepède [syn. *Pimelodus clarias* (Linnaeus)].
SI: Intestine. Lo: Río Paraná Medio, Corrientes Province. MD: Not indicated. DS: Adults and third- and fourth-stage larvae. Reference: Hamann (1985). SI: Intestine. Lo: San Javier River (31°13'S, 60°10'W), Cayastá; Feller Lagoon (31°01'S, 60°01'W); San Javier River, Helvecia, Santa Fé Province. MD: MFA-ZI-N-233. DS: Adults. Reference: Chemes & Takemoto (2020).

Host *Pimelodus albicans* (Valenciennes)
SI: Intestine. Lo: Paraná Medio River, Corrientes Province. MD: Not indicated DS: Adults. Reference: Hamann (1985). SI: Intestine. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Santiago del Estero-Tucuman Provinces. MD: CH-N-FML # 01840. DS: Adults. Reference: Ramallo (1999). SI: Stomach. Lo: Pilcomayo River (22°22'S, 62°32'W), Salta Province. MD: CH-N-FML # 7775. DS: Adults. Reference: Ramallo *et al.* (2020).

Host *Pseudoplatystoma corruscans* (Spix & Agassiz)
SI: Intestine. Lo: Río Paraná Medio, Corrientes Province. MD: Not indicated. DS: Adults and third- and fourth-stage larvae. Reference: Hamann (1985).

Host *Trichomycterus spegazzinii* (Berg) **
SI: Intestine. Lo: Strem affluent of Yacones River (24°31'S, 65°24'W), Isasmendi Stream (24°48'S, 64°26'W), Salta Province. MD: UNSa-IEBI-I # 050. DS: Adults. Reference: Ailán-Choke *et al*. (2014). SI: Intestine. Lo: La Caldera River (24°35'S, 65°22'W), Yacones River (24°40'S, 65°24'W) Salta Province. MD: UNSa-IEBI-I # 060. DS: Adults. Reference: Present study. Remarks: New locality record.

Genus *Dichelyne* Jägerskiöld, 1902
Subgenus *Cucullanellus* (Tornquist, 1931)
***Dichelyne* (*Cucullanellus*) *mariajuliae* Alarcos *et al.*, 2006**

Host *Pogonias cromis* (Linnaeus)
SI: Middle and posterior intestine. Lo: Mar Chiquita coastal lagoon (37°32'S, 57°19'W), Buenos Aires Province. MD: (H) CHMLP # 5520; (A) CHMLP # 5521; (P) CHMLP # 5522. DS: Adults (males and females). Reference: Alarcos *et al*. (2006).

Genus *Neocucullanus* Travassos, Artigas & Pereira, 1928
***Neocucullanus marcelae* Ramallo, 2012**

Host *Salminus brasiliensis* (Cuvier, 1816)
SI: Intestine, pyloric caeca and liver. Lo: El Chorro, Juramento River (25°13'S, 64°28'W), Salta Province. MD: (H): CH-N-FML# 07488; (A): CH-N-FML #07489; (P) CH-N-FML # 07490. DS: Adults. Reference: Ramallo (2012).

Order Spirurida
Superfamily Camallanoidea
Family Camallanidae
Genus *Camallanus* Railliet & Henry, 1915

Synonym: *Zeylanema* Yeh, 1960

Subgenus *Zeylanema* Yeh, 1960
***Camallanus (Zeylanema) corderoi* Torres, Teuber & Miranda, 1990**

Host *Galaxias maculatus* (Jenyns)
SI: Intestine. Lo: Nahuel Huapi Lake (41°03'S, 71°25'W), Neuquén and Río Negro Provinces. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994). SI: Intestine. Lo: Moreno Lake (41°04'S, 71°33'W), Neuquen Province. MD: Not indicated. DS: Not indicated. Reference: Rauque *et al.* (2003). SI: Intestine. Lo: Senillosa Channel (Limay River) (38°50'S, 68°30'W); Lakes: Ñorquinco (39°09'S, 71°17'W), Huechulafquén (39°45'S, 71°25'W), Morenito (41°05'S, 71°31'W), and Escondido (41°05'S, 71°35 W); and Caleufu River (40°30'S, 71°17'W), Patagonia. MD: MACN-Pa 463. DS: Larvae. Reference: Viozzi *et al.* (2009). SI: Intestine. Lo Nahuel Huapi Lake (41°04'S, 71°25'W), Neuquén and Río Negro Provinces. MD: Not indicated. DS: Larvae. Reference: Fernandez *et al.* (2015). Remarks: The records of *Camallanus* (*Zeylanema*) *corderoi* larvae has to be carefully reviewed, because their morphology does not enable to identify them to species. *Camallanus* (*Zeylanema*) *corderoi* is a common parasite of *Percichthys trucha*. According to Rauque *et al.* (2018), *C. corderoi* uses the native *G. maculatus* as intermediate host and the native *P. trucha* as definitive.

Host *Galaxias platei* Steindachner
SI: Intestine. Lo: Ezquerra Lagoon (41°03'S, 71°33'W), Río Negro Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994). SI: Intestine. Lo: Moreno Lake (41°04'S, 71°33'W), Neuquen Province. MD: Not indicated. DS: Not indicated. Reference: Rauque *et al.* (2003).

Host *Jenynsia multidentata* (Jenyns) ▪
SI: Intestine. Lo: Arroyón Stream (38°43.66′S 68°02.4′W), Neuquén River, Neuquén Province. MD: MACN–Pa 657/1. DS: non-gravid adults. Reference: Rauque *et al.* (2018).

Host *Odontesthes bonariensis* (Valencienne)
SI: Intestine. Lo: Pellegrini Lake (38°41'S, 68°00'W), Neuquén River, Neuquén Province. MD: MACN–Pa 657/1. DS: gravid adults. Reference: Rauque *et al.* (2018).

Host *Odontesthes hatcheri* (Eigenmann) (syn. *Patagonina hatcheri*).
SI: intestine. Lo: Alicurá Reservoir, Río Negro-Neuquén Provinces, Pellegrini Lake, Río Negro Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.*, 1994. SI: Intestine. Lo: Marimenuco Reservoir (38°32'S, 69°25'W), Neuquén province; Lezana Lake (42°27'S, 71°29'W) and Musters Lake (45°25'S, 69°11'W), Chubut Province; Morenito lake (41°02'S, 68°34'W) and Moreno Oeste Lake (41°06'S, 71°32'W), Río Negro Province. MD: CHMLP. DS: Adults. Reference: Flores *et al.* (2016).

Host *Oncorhynchus mykiss* (Walbaum)
SI: intestine. Lo: Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994). SI: Intestine. Lo: Moreno Lake (41°04'S, 71°33'W), Neuquen Province. MD: Not indicated. DS: Not indicated. Reference: Rauque *et al.* (2003). SI: Intestine. Lo: El Chañar Reservoir (38°34.5'S, 68°24'W), Neuquén River; Escondido Lake (41°42'S, 71°38'W), Morenito Lake (41°03'S 71°31'W), Moreno Lake (41°05'S, 71°30'W), Nahuel Lake (41°05'S, 71°20'W), Ramos Mexía Reservoir (39°26'S, 68°56'W), downstream Arroyito Dam (39°04.5'S, 68°33'W), all Limay River, Río Negro Province. MD: MACN–Pa 657/1. DS: non-gravid adults. Reference: Rauque *et al.* (2018).

Host *Percichthys trucha* (Valenciennes)
SI: Stomach, intestine, pyloric caecum. Lo: Moreno (41°06'S, 71°32'W) and Pellegrini (38°40'S, 68°00'W) Lakes, Ezquerra Lagoon (41°03'S, 71°33'W); Casa de Piedra Stream (38°10'S, 67°30'W) and Alicurá Reservoir (40°40'S, 71°00'W), Río Negro-Neuquén Provinces. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994) and Rauque *et al.* (2003).

Host *Salmo salar* Linnaeus
SI: Intestine. Lo: Alicurá Reservoir (40°35'S, 70°50'W), Limay River, Río Negro Province. MD: MACN–Pa 657/1. DS: non-gravid adults. Reference: Rauque *et al.* (2018).

Host *Salmo trutta* Linnaeus
SI: Intestine. Lo: Moreno Lake (41°05'S, 71°30'W); Gutiérrez Lake (41°12'S, 71°24.5'W), Nahuel Huapi Lake (41°05'S, 71°20'W), Alicurá Reservoir (40°35'S, 70°50'W), Piedra del Águila Reservoir (40°19'S, 70°03'W), Pichi Picún Leufú Reservoir (40°01'S, 70°00'W), all Limay River, Río Negro Province. MD: MACN–Pa 657/1. DS: non-gravid adults. Reference: Rauque *et al.* (2018).

Host *Salvelinus fontinalis* (Mitchill)
SI: Intestine. Lo: General Vintter Lake (43°52'S, 71°30'W) and Corcovado River (40°40'S, 71°00'W), Chubut Province. MD: Not indicated. DS: Not indicated. Reference: Úbeda *et al.* (1989). SI: Intestine. Lo: Moreno Lake (41°04'S, 71°33'W), Neuquen Province. MD: Not indicated. DS: Not indicated. Reference: Rauque

et al. (2003). SI: Intestine. Lo: Moreno Lake (41°05'S, 71°30'W), Limay River, Río Negro Province. MD: MACN–Pa 657/1. DS: non-gravid adults. Reference: Rauque *et al.* (2018).

Subgenus *Camallanus* Railliet & Henry, 1915
***Camallanus* (*Camallanus*) *tridentatus* (Drasche, 1884)**

Synonym: *Cucullanus tridentatus* Drasche, 1884
Host *Oncorhynchus mykiss* (Walbaum) ◦
SI: Intestine. Lo: Lezama Lake, Chubut Province. MD: Not indicated. DS: Adults. Reference: Úbeda *et al.* (1989).

Host *Percichthys colhuapiensis* MacDonagh
SI: Not indicated. Lo: Ezequiel Ramos Mexia Reservoir (39°30'S, 69°00'W), Río Negro-Neuquén Provinces. MD: Not indicated. DS: Not indicated. Reference: Ortubay *et al*. (1994).

Host *Percichthys trucha* (Valenciennes) ◦
SI: Pyloric caecum, small intestine and stomach. Lo: Pellegrini Lake (38°40'S, 68°00'W), Río Negro Province. MD: Not indicated. DS: Adults. Reference: Szidat (1956). SI: Intestine and stomach. Lo: Mosquito Lagoon and Lezama Lake, Chubut Province. MD: Not indicated. DS: Adults. Reference: Úbeda *et al.* (1989).

Host *Salvelinus fontinalis* (Mitchill) ◦
SI: Intestine. Lo: Winter Lake and Corcovado River, Chubut Province. MD: Not indicated. DS: Adults. Reference: Úbeda *et al*. (1989). Remarks: According to Ortubay *et al*. (1994), *C. tridentatus* reported on *O. mykiss*, *P. trucha*, and *S. fontinalis* (Úbeda *et al*., 1989), was misidentified and could correspond to *Camallanus corderoi*.

Genus *Procamallanus* Baylis, 1923
Subgenus *Denticamallanus* Moravec & Thatcher, 1997
***Procamallanus* (*Denticamallanus*) *ana* Ramallo, 2011**

Host *Thoracocharax stellatus* (Kner)
SI: Intestine. Lo: Teuquito River (24°12'S, 62°54'W), Salta Province. MD: (H) CH-N-FML # 07475; (A) CH-NFML # 07476, and (P) CH-N-FML # 07477. DS: Adults. Reference: Ramallo (2011).

Genus *Spirocamallanus* Olsen, 1952
***Spirocamallanus hilarii* Vaz & Pereira, 1934**

Synonyms: *Procamallanus cearensis* Pereira, Dias & Azevedo, 1936; *Spirocamallanus incarocai* Freitas & Ibañez, 1970.
Host *Astyanax abramis* (Jenyns)
SI: Intestine and stomach. Lo: (27°33'S, 64°57'W), Tucumán and Santiago del Estero Provinces. MD: Not indicated. DS: Adults. Reference: Ramallo (2005a).

Host *Astyanax bimaculatus* (Linnaeus)
SI: Intestine and stomach. Lo: Escaba Dam (27°42'S, 64°48'W), Río Hondo Reservoir (27°33'S, 64°57'W), Tucumán and Santiago del Estero Provinces. MD: CH-N-FML # 04018 for record from Escaba Dam. DS: Adults. Reference: Ramallo (2005a). SI: Intestine and stomach. Lo: El Tunal Reservoir (25°14'S, 64°31'W), Salta Province. MD: Not indicated. DS: Adults. Reference: Cancino & Ramallo (2008). SI: Intestine and stomach. Lo: Itaú River (22°20'S, 64°05'W). MD: CH-N-FML #07480. DS: Adults. Reference: Antelo *et al.* (2016). Remarks: Host originally reported as *Astyanax bimaculatus*, but according to Lucena & Soares (2016) the material identified as *A. bimaculatus* corresponds to *A. lacustris*.

Host *Bryconamericus thomasi* Fowler (syn. *Piabina thomasi*) **
SI: Intestine. Lo: Itaú River (22°20'S, 64°05'W), Salta Province. MD: Not indicated. DS: Adults. Reference: Antelo *et al*. (2016). SI: Intestine. Lo: Arias River (24°47'S, 65°28'W), Arias-Arenales River (24°48'S, 65°25'W), San Lorenzo River (24°47'S, 65°28'W), Salta Province. MD: UNSa-IEBI-I # 0051. DS: Adults. Reference: Present study. Remarks: new locality records.

Host *Psalidodon anisitsi* (Eigenmann) (syn. *Hyphessobrycon anisitsi*)
SI: Intestine. Lo: Salado River (28°48'S, 62°39'W), Añatuya, General Taboada Department, Santiago del Estero Province. MD: CH-N-FML # 7732. DS: Adults. Reference: Ramallo & Ailán-Choke (2017).

Host *Hoplias misionera* Rosso *et al*.
SI: Intestine and stomach. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: Not indicated. DS: Adults. Reference: Ramallo (1997).

Host *Jenynsia alternimaculata* (Fowler)
SI: Intestine. Lo: Isasmendi Stream (24°48'S, 65°26'W); Yacones River (24°40'S, 65°24'W), Salta Province. MD: CH-N-FML # 7513; UNSa-IEBI-I # 0051. DS: Adults. Reference: Ailán-Choke *et al.* (2014).

Host *Megaleporinus obstusidens* Valenciennes (syn. *Leporinus obtusidens*)
SI: Intestine and stomach. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: Not indicated. DS: Adults. Reference: Ramallo (1997).

Host *Oligosarcus jenynsii* (Günther)
SI: Intestine and stomach. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: Not indicated. DS: Adults. Reference: Ramallo (1997).

Host *Pimelodus albicans* (Valenciennes)
SI: Intestine and stomach. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: CH-N-FML # 01937. DS: Adults. Reference: Ramallo (1997).

Host *Psalidodon eigenmanniorum* (Cope) (syn. *Astyanax eigenmanniorum*) ***
SI: Intestine. Lo: Arias River (24°47'S, 65°28'W), Arias-Arenales River (24°48'S, 65°25'W), San Lorenzo River (24°47'S, 65°28'W), Salta Province. MD: UNSa-IEBI-I # 0051. DS: Adults. Reference: Present study. Remarks: New host and locality records.

Host *Psalidodon endy* (Mirande, Aguilera & Azpelicueta) (syn. *Astyanax endy*) ***
SI: Intestine. Lo: La Caldera River (24°35'S, 65°22'W), La Calderilla Stream (24°39'S, 65°22'W), Campo Alegre Dam (24°34'S, 65°21'W) Salta Province. MD: UNSa-IEBI-I N°0051. DS: Adults. Reference: Present study. Remarks: New host and locality records.

Host *Psalidodon rutilus* (Jenyns) [syn. *Astyanax fasciatus* (non Cuvier, 1819)]
SI: Intestine and stomach. Lo: Río Hondo Reservoir (27°33'S, 64°57'W), Tucumán and Santiago del Estero Provinces. MD: CH-N-FML # 07426. DS: Adults. Reference: Ramallo (2005a).

Host *Salminus brasiliensis* (Cuvier) **
SI: Intestine and stomach. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: CH-N-FML #01301. DS: Adults. Reference: Ramallo (1997). SI: Intestine. Lo: Juramento River (25°13'S, 64°28'W), Salta Province. MD: CH-N-FML #07800 and 07801. DS: Adults. Reference: Present study. Remarks: New locality record.

Host *Trichomycterus spegazzini* (Berg) ***
SI: Intestine. Lo: La Caldera River (24°35'S, 65°22'W), Salta Province. MD: UNSa-IEBI-I # 0051. DS: Adults. Reference: Present study. Remarks: New host and locality records.

Spirocamallanus huacraensis Ramallo, 2008

Host *Trichomycterus corduvensis* Weyenbergh
SI: Intestine. Lo: Huacra River (28°00'S, 65°33'W), Catamarca Province. MD: (H) CH-N-FML #07432, (A) CH-N-FML # 07431, (P) CH-N-FML #07433. DS: Adults. References: Ramallo (2008). SI: Intestine. Lo: Vis-Vis River (27°15'S, 66°35'W), Catamarca Province. MD: CH-N-FML # 07478. DS: Adults. Reference: Ramallo & Padilla Bortayro (2011).

Host *Trichomycterus spegazzinii* (Berg)
SI: Intestine. Lo: Escoipe River (25°06'S, 65°36'0.4" W) Salta. MD: MACN-Pa N°662. DS: Adults. Reference: Ailán-Choke *et al*. (2019).

Spirocamallanus inopinatus Travassos, Artigas & Pereira, 1928

Synonyms: *Procamallanus fariasi* Pereira, 1935; *P. wrighti* Pereira, 1935; *P. probus* Pinto & Fernandes, 1972.

Host *Brycon orbignyanus* (Valenciennes)
SI: Intestine. Lo: Middle Paraná River and Santa Lucía River, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986).

Host *Poptella paraguayensis* (Eigenmann) (syn. *Ephippicharax orbicularis paraguayensis*)
SI: Intestine. Lo: Middle Paraná River and Santa Lucía River, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986).

Host *Hoplias misionera* Rosso *et al*.
SI: Intestine. Lo: Pilcomayo River (22°22'S, 62°32'W) Rivadavia Department, Salta Province. MD: CH-N-FML # 7776. DS: Adults. Reference: Ramallo *et al.* (2020).

Host *Megaleporinus obtusidens* (Valenciennes)
SI: Intestine. Lo: Middle Paraná River and Santa Lucía River, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986).

Host *Leporinus maculatus* Müller & Troschel •
SI: Intestine. Lo: Midle Paraná River and Santa Lucía River, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986). Remarks: *Leporinus maculatus* is not occurring in Argentina (Mirande & Koerber, 2020), but according to Braga (1993) and López *et al.* (2003), the records of this species could correspond to *Leporinus acutidens*.

Host *Luciopimelodus pati* (Valenciennes)
SI: Intestine. Lo: Midle Paraná River and Santa Lucía River, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986).

Host *Pimelodus maculatus* Lacépède
SI: Intestine. Lo: Coronda River (31°41'S, 60°44'W), Santo Tomé, Santa Fé Province. MD: MFA-ZI-N-232. DS: Only one male. Reference: Chemes & Takemoto (2020).

Host *Pseudoplatystoma corruscans* (Spix & Agassiz)
SI: Intestine. Lo: Middle Paraná River and Santa Lucía River, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986).

Host *Pygocentrus nattereri* Kner (syn. *Serrasalmus nattereri*).
SI: Intestine. Lo: Perez and Totora Lagoons, Riachuelo Basin, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986).

Host *Serrasalmus marginatus* Valenciennes
SI: Intestine. Lo: Perez and Totora Lagoons, Riachuelo Basin, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986).

Host *Serrasalmus spilopleura* Kner •
SI: Intestine. Lo: Perez and Totora Lagoons, Riachuelo Basin, Corrientes Province. MD: Not indicated. DS: Not indicated. Reference: Hamann (1986). Remarks: According to Mirande & Koerber (2020), *S. spilopleura* is not present in Argentina, but this record could correspond to *Serrasalmus maculatus* Kner (Jégu & Santos, 2001; Mirande & Koerber, 2020).
SI: Intestine. Lo: Aeroclub and Ramada Lagoons, Riachuelo River basin, Corrientes Province. MD: Not indicated. DS: Adults. Reference: Hamann (1995/1996).

Spirocamallanus juana Ramallo & Ailán Choke, 2017

Host *Pimelodus albicans* (Valenciennes)
SI: Intestine. Lo: Salado River (28°48'S, 62°39'W) Santiago del Estero Province. MD: (H) CH-N-FML # 07729; (A) CH-N-FML # 07730; (P) CH-N-FML # 07731. DS: Adults. Reference: Ramallo & Ailán-Choke (2017).

Host *Pimelodella gracilis* (Valenciennes)
SI: Intestine. Lo: Salado River (28°48'S, 62°39'W) Santiago del Estero Province. MD: Not indicated. DS: Adults. Reference: Ramallo & Ailán-Choke (2017).

Spirocamallanus neocaballeroi (Caballero-Deloya, 1977)

Host *Pimelodus maculatus* Lacépède
SI: Intestine. Lo: lag Feller Lagoon (31°01'S, 60°01'W), San Javier River, Helvecia, Santa Fé Province. MD: MFA-ZI-N-231. DS: Only one male. Reference: Chemes & Takemoto (2020).

Spirocamallanus pimelodus Pinto, Fábio, Noronha & Rolas, 1974

Synonym: *Procamallanus intermedius* Pinto, Fábio, Noronha & Rolas, 1974.

Host *Pimelodus maculatus* Lacépède
SI: Intestine. Lo: Feller Lagoon (31°01'S, 60°01'W), San Javier River, Helvecia, Santa Fé Province. MD: MFA-ZI-N-234. DS: Adults. Reference: Chemes & Takemoto (2020).

Spirocamallanus pintoi (Kohn & Fernandes, 1988)

Host *Trichomycterus spegazzinii* (Berg)
SI: Intestine. Lo: Isasmendi Stream (24°48'S, 65°26'W), Salta Province. MD: CH-N-FML #7515. DS: Adult. Reference: Ailán-Choke *et al*. (2014).

Host *Corydoras paleatus* (Jenyns)
SI: Intestine. Lo: Arias-Arenales River (24°48'S, 65°25'W) and Arias River (24°47'S, 65°28'W) Salta Province. MD: CH-FML # 7739. DS: Adults. Reference: Ailán-Choke *et al.* (2018).

Host *Corydoras micracanthus* Regan
SI: Intestine. Lo: Yacones River (24°40'S, 65°24'W) and Lesser River (24°39'S, 65°28'W), Salta Province. MD: CH-FML # 7740. DS: Adults. Reference: Ailán-Choke *et al.* (2018).

Spirocamallanus rarus Travassos, Artigas & Pereira, 1928

Synonym: *Spirocamallanus rarus* Olsen, 1952
Host *Pimelodus albicans* (Valenciennes)
SI: Small and large intestine. Lo: Middle Paraná River, Corrientes Province. MD: CECOAL. DS: Adults. Reference: Hamann (1984).

Spirocamallanus tomsici Ramallo & Ailán Choke, 2020

Host *Pimelodus albicans* (Valenciennes)
SI: Intestine. Lo: Misión La Paz, Pilcomayo River (22°22'S, 62°32'W), Rivadavia Department, Salta Province. MD: (H) CH-N-FML #07766; (A) CH-N-FML # 07767; (P) CH-N-FML # 07768. DS: Adults. Reference: Ramallo *et al.* (2020).

Host *Pygocentrus nattereri* Kner
SI: Intestine. Lo: Misión La Paz, Pilcomayo River (22°22'S, 62°32'W), Rivadavia Department, Salta Province. MD: CH-N-FML #07788. DS: Adults. Reference: Ramallo *et al.* (2020).

Host *Hoplias misionera* Rosso *et al*.
SI: Intestine. Lo: Misión La Paz, Pilcomayo River (22°22'S, 62°32'W), Rivadavia Department, Salta Province. MD: CH-N-FML # 7789. DS: Adults. Reference: Ramallo *et al.* (2020).

Superfamily Cosmocercoidea
Family Atractidae
Genus *Klossinemella* Costa, 1961
***Klossinemella iheringi* (Travassos, Artigas & Pereira, 1928)**

Synonym: *Monhysterides iheringi* Travassos, Artigas & Pereira, 1928
Host *Pterodoras granulosus* (Valenciennes)
SI: Intestine. Lo: Paraná River, Corrientes Province. MD: CECOAL. DS: Adults. Reference: Hamann (1982b).

Genus *Rondonia* Travassos, 1920
***Rondonia rondoni* Travassos, 1920**

Host *Piaractus mesopotamicus* (Holmberg) [syn. *Colossoma mitrei* (Berg)].
SI: Intestine. Lo: Paraná Medio River, Corrientes Province. MD: CECOAL. DS: Adults. Reference: Hamann (1982a).

Host *Pterodoras granulosus* (Valenciennes)
SI: Intestine. Lo: Parana Medio River, Corrientes Province. MD: CECOAL. DS: Adults. Reference: Hamann (1982b).

Family Kathlaniidae
Genus *Spectatus* Travassos, 1923
***Spectatus spectatus* Travassos, 1923**

Host *Piaractus mesopotamicus* (Holmberg) (syn. *Colossoma mitrei*).
SI: Intestine. Lo: Paraná Medio River, Corrientes Province. MD: CECOAL. DS: Adults. Reference: Hamann (1982a).

Host *Pterodoras granulosus* (Valenciennes)
SI: Intestine. Lo: Paraná Medio River, Corrientes Province. MD: CECOAL. DS: Adults. Reference: Hamann (1982b).

Superfamily Dracunculoidea
Family Guyanemidae
Genus *Pseudodelphis* Adamson & Roth, 1990
***Pseudodelphis limnicola* Brugni & Viozzi, 2006**

Host *Percichthys trucha* (Valenciennes)
SI: Sinus venosus and atrium, intestine, and abdominal cavity. Lo: Lake Escondido (41°05'S, 71°35'W), Nahuel Huapi National Park, Río Negro Province. MD: MACNPa (H) # 429/1; (A) # 429/2, (P) # 429/3–6 and 429/7–10; CHMLP (P) # 5519; UNCo-Pa (P) # 201/1–10 and (P) 201/11–20) and IPCAS Helm. (P) # N833 (1 male and 1 female). DS: Adult males and gravid females, larvae and sub-adults. Reference: Brugni & Viozzi (2006).

Family Philometridae
Genus *Philonema* Kuitunen-Ekbaum, 1933

Synonym: *Coregonema* Bauer, 1946
***Philonema percichthydis* Moravec, Urawa & Coria, 1997**

Host *Percichthys trucha* (Valenciennes)
SI: Abdominal cavity. Lo: Lago Aluminé, (38°55'S, 71°10'W), Río Negro basin, Río Negro Province. MD: IPCAS Helm. (holotype and remnants of paratypes, Cat. # N-690. DS: Two gravid females. Reference: Moravec *et al.* (1997b).

Superfamily Habronematoidea
Family Cystidicolidae
Genus *Ascarophis* van Beneden, 1871

Synonyms: *Capillospirura* Skrjabin, 1924; *Pseudocystidicola* Layman, 1933

***Ascarophis patagonica* Brugni & Viozzi, 2008**

Host *Galaxias platei* Steindachner
SI: Stomach. Lo: Moreno Lake (41°05'S, 71°32'W), Coyte Pond (45°25'S, 71°22'W), Río Negro Province. MD: MACN (H) # 442/1, (A) # 442/2, (P) #442/3-7 and # 442/8-12; CPUNCo (P) #5756; CHMLP (P) # 215/1-7 and # 215/8-14 and USNPC (P) #100568. DS: Males and gravid females. Reference: Brugni & Viozzi (2008).

Genus *Placonema* Brugni, Viozzi, Fernández & Vega, 2009
***Placonema pataguense* Brugni, Viozzi, Fernández & Vega, 2009**

Host *Galaxias maculatus* (Jenyns)
SI: Stomach. Lo: Patagua Lake (40°47'S, 71°37'W), Arrayanes National Park, Río Negro Province. MD: MACN-Pa: (H) male # 446/1), (A) female # 446/2, and (P) # 446/3–5 and # 446/6–8. USNPC (P) #101088, # 101090, #101087, # 101089). UNC (P) # 216/1–5 and # 216/6–12. MLP (P) # 5865. DS: Adults. Reference: Brugni *et al.* (2009).

Genus *Spinitectus* Fourment, 1883
***Spinitectus asperus* Travassos, Artigas & Pereira, 1928**

Synonym: *Spinitectus jamundensis* Thatcher & Padilha, 1977
Host *Prochilodus lineatus* (Valenciennes) (syn. *P. platensis* Holmberg)
SI: Stomach. Lo: Middle Paraná River, Corrientes Province. MD: CECOAL. DS: male and gravid females. Reference: Hamann (1982c). SI: Cardial stomach. Lo:

Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: CH-N-FML # 01298. DS: males, gravid females and larvae. Reference: Ramallo (1999). SI: Cardial stomach. Lo: Misión La Paz, Pilcomayo River (22°22'S, 62°32'W), Rivadavia Department, Salta Province. MD: CH-N-FML #07773. DS: Adults. Reference: Ramallo *et al.* (2020).

Host *Pimelodus albicans* (Valenciennes)
SI: Posterior intestine. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: Not indicated. DS: Adults. Reference: Ramallo (1999).

Host *Megaleporinus obstusidens* Valenciennes
SI: Posterior intestine. Lo: Río Hondo Reservoir (27°31'S, 64°53'W), Tucumán-Santiago del Estero Provinces. MD: Not indicated. DS: Adults. Reference: Ramallo (1999).

Family Hedruridae
Genus *Hedruris* Nitzsch, 1821
***Hedruris* sp.**

Host *Galaxias maculatus* (Jenyns)
SI: Abdominal cavity. Lo: Moreno Lake (41°03'S 71°31'W), Río Negro Province. MD: Not indicated. DS: Larvae. Reference: Revenga *et al.* (2005). SI: Stomach. Lo: Lakes Ñorquinco (39°09'S, 71°17'W), Quillén (39°25'S, 71°20'W), Tromen (39°32'S, 71°28'W); Machónico (40°20'S, 71°33'W), Hermoso (40°21'S, 71°28'W), Pudú Pudú (40°23'S, 71°28'W), Villarino (40°28'S, 71°35'W), Falkner (40°29'S, 71°29'W), Filo Hua Hum (40°30'S, 71°17'W), Espejo Chico (40°35'S, 71°44'W), Traful (40°37'S, 71°25'W), Espejo (40°41'S, 71°40'W), Correntoso (40°44'S, 71°39'W), Patagua (40°47'S, 71°37'W), Morenito (41°05'S, 71°31'W); Mascardi (41°17'S, 71°38'W), Fonck (41°18'S, 71°43'W), Hess (41°22'S, 71°43'W), Steffen (41°31'S, 71°33'W), Patagonia. MD: MACN-Pa 466. DS: Adults. Reference: Viozzi *et al*. (2009).

Host *Galaxias platei* Steindachner
SI: Not indicated. Lo: Lagoons: Zeta (42°53'S, 71°20'W), Caradogh Jones (42°54'S, 71°23'W), Huillimanco (42°52'S, 71°17'W); Rosario Lake (43°15'S, 71°20'W), Chubut Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al*. (1994). SI: Stomach. Lo: Lakes: Cholila (42°27'S, 71°40'W), and Esperanza (42°13'S, 71°50'W), Chubut Province, and Pueyrredón Lake (47°16'S, 72°00'W), Santa Cruz Province; Lagoons: Huillimanco (42°52'S, 71°50'W), and La Pava, Chubut Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994).

Host *Oncorhynchus mykiss* (Walbaum)
SI: Stomach, intestine, pyloric caecum. Lo: Casa de Piedra (38°10'S, 67°30'W) Stream, Ñireco River (41°14'S, 71°11'W), Limay River and Nahuel Huapi Lake (41°03'S, 71°25'W), Río Negro Province. MD: Not indicated. DS: Adults and larvae. Reference: Ortubay *et al*. (1994). SI: Not indicated. Lo: Ñireco River (41°14'S, 71°11'W), Río Negro Province; Traful Lake (40°37'S, 71°25'W), Neuquén Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994).

Host *Percichthys trucha* (Valenciennes)
SI: Stomach. Lo: Ñireco River, Río Negro Province. MD: Not indicated. DS: Adults and larvae. Reference: Ortubay *et al.* (1994). SI: Stomach. Lo: Moreno Lake (42°27'S, 71°40'W), Río Negro Province; Cholila Lake (42°27'S, 71°40'W), Chubut Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al*. (1994).

Host *Salmo trutta* Linnaeus
SI: Stomach. Lo: Hess Lake (41°22'S, 71°43'W), Río Negro Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994). SI: Stomach. Lo: Limay River (41°22'S, 71°43'W), Río Negro-Neuquén Provinces. MD: Not indicated. DS: Adults and larvae. Reference: Ortubay *et al.* (1994). Remarks: Rauque *et al.* (2018) mentioned that records of *Hedruris* sp. in *O. mykiss*, *S. trutta*, *G. maculatus*, *G. platei* and *P. trucha*, could correspond to *Hedruris suttonae*.

***Hedruris bifida* Rossin & Timi, 2016**

Host *Oligosarcus jenynsii* (Günther)
SI: Females attached to stomach wall and males generally found encircling female. Lo: Lake Nahuel Rucá (37°37'S, 57°26'W), Buenos Aires Province. MD: (H) (MLP-He coll. # 7159), (A) (MLP-He coll. # 7160) and (P) MLP-He coll. # 7161. DS: Adults (males and females). Reference: Rossin & Timi (2016).

***Hedruris suttonae* Brugni & Viozzi, 2010**

Host *Galaxias maculatus* (Jenyns)
SI: Stomach. Lo: Lakes: Moreno (41°03'S, 71°31'W), Ñorquinco (39°09'S, 71°17'W), Quillén (39°25'S, 71°25'W), Tromen (39°32'S, 71°27'W), Machónico (40°21'S, 71°26'W), Pudú Pudú (40°23'S, 71°28'W), Hermoso (40°23'S, 71°29'W), Villarino (40°28'S, 71°35'W), Falkner (40°29'S, 71°29'W), Filo Hua Hum (40°30'S, 71°17'W), Traful (40°37'S, 71°25'W), Espejo (40°41'S, 71°40'W), Espejo Chico (40°41'S, 71°42'W), Correntoso (40°44'S, 71°39'W), Nahuel Huapi (40°48'S, 71°39'W), Patagua (40°51'S, 71°50'W), Moreno (41°03'S, 71°31'W), Mascardi (41°17'S, 71°38'W), Fonck (41°19'S, 71°45'W), Hess (41°23'S, 71°43'W), Steffen (41°31'S, 71°33'W), Patagonia. MD: MACN-Pa

(H) and (A) # 406-1 and (P) # 406-2; UNCo-Pa (P) #129 ; CHLMP (P) # 4927 (5 males and 8 females), and USNPC (P) # 102470. DS: Females attached to mucosa by caudal hook, males free or coiled around females (sometimes more than 1 for each female). Reference: Brugni & Viozzi (2010).

Host *Galaxias platei* Steindachner
SI: Stomach. Lo: Lakes: Moreno (41°03'S, 71°31'W), Cisne (42°36'S, 71°56'W) and Coyte (45°15'S, 71°12'W), Patagonia. MD: Not indicated. DS: Not indicated. Reference: Brugni & Viozzi (2010).

Host *Oncorhynchus mykiss* (Walbaum)
SI: Stomach. Lo: Moreno Lake (41°05'S, 71°30'W), Nahuel Huapi Lake (41°05'S, 71°20'W), Limay River; Musters Lake (45°33'S, 69°15'W) Senguer River, Río Negro-Chubut Provinces. MD: MACN–Pa 656/1. DS: gravid adults. Reference: Rauque *et al.* (2018).

Host *Salmo trutta* Linnaeus
SI: Stomach. Lo: Nahuel Huapi (41°05'S, 71°20'W), Limay River, Río Negro Provinces. MD: MACN–Pa 656/1. DS: gravid adults. Reference: Rauque *et al.* (2018).

Host *Salvelinus fontinalis* (Mitchill)
SI: Stomach. Lo: Moreno Lake (41°05'S, 71°30'W), Nahuel Huapi Lake (41°05'S, 71°20'W), Limay River; Cholila Lake (42°27.5'S, 71°40'W), Futaleufú River, Río Negro-Chubut Provinces. MD: MACN–Pa 656/1. DS: gravid adults. Reference: Rauque *et al*. (2018). Remarks: Adult nematodes of *H. suttonae* were originally described from *G. maculatus* and *G. platei* from Patagonia (Brugni & Viozzi, 2010; Rauque *et al.,* 2018). Brugni & Viozzi (2010) reported that the intermediate host of this parasite is the amphipod *Hyalella patagonica*. Thus, its presence in salmonids probably represent a case of spillback (Rauque *et al.,* 2018).

Superfamily Thelazioidea
Family Rhabdochonidae
Genus *Rhabdochona* Railliet, 1916

Synonyms: *Ichthyospirura* Skrjabin, 1917; *Pseudorhabdochona* Liu & Wu, 1941; *Filochona* Saidov, 1953; *Rhabdochonoides* Janiszewska, 1955; *Afrochona* Puylaert, 1973.

***Rhabdochona* sp.**

Host *Galaxias platei* Steindachner
SI: Stomach. Lo: Zeta Lagoon (42°53'S, 71°20'W), Santa Cruz River, Chubut Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al*. (1994).

Host *Odontesthes hatcheri* (syn. *Patagonina hatcheri*)
SI: Intestine. Lo: Rosario Lake, Chubut Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994).

Host *Oncorhynchus mykiss* (Walbaum)
SI: Gastrointestinal tract. Lo: Zeta Lagoon (42°53'S, 71°20'W), Santa Cruz River, Chubut Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994). Remarks: The records of *Rhadochona* sp. in *G. platei*, *O. hatcheri* and *O. mykiss* could correspond to *Rhadochona acuminata* (Molin, 1860), since this parasite has been cited in many freshwater fishes from Patagonia.

***Rhabdochona acuminata* (Molin, 1860)**

Synynonyms: *Spiroptera acuminata* Molin, 1860; *Rhabdochona elegans* Travassos, Artigas & Pereira, 1928; *R. fasciata* Kloss, 1966; *R. australis* Kloss, 1966; *R. siluriformis* Kloss, 1966.

Host *Astyanax lacustris* (Luetken)
SI: Intestine. Lo: El Tunal Dam (25°15'S, 64°25'W) Salta Province. MD: Not indicated. Reference: Cancino & Ramallo (2008).

Host *Olivaichthys mesembrinus* (Ringuelet) (syn. *Diplomystes mesembrinus*).
SI: Intestine. Lo: Río Chubut, Chubut Province (43°39'-43°53'S, 66°22'-68°24'W). MD: MACN-Pa #37. DS: adults and third and fourth stage larvae. Reference: Cremonte *et al.* (2002).

Host *Galaxias maculatus* (Jenyns)
SI: Intestine. Lo: Nahuel Huapi Lake, Río Negro Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al.* (1994). SI: Intestine. Lo: Río Chubut (43°39'-43°53'S, 66°22'-68°24´W) Chubut Province. MD: Not indicated. DS: Adults and third- and fourth-stage larvae. Reference: Cremonte *et al*. (2002).

Host *Galaxias platei* Steindachner
SI: Intestine. Lo: Ezquerra lagoon (41°03'S, 71°33'W) Santa Cruz Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al*. (1994).

Host *Hatcheria macraei* (Girard) (syn. *Thrichomycterus macraei*).
SI: Intestine. Lo: Castaño River, San Juan Province. MD: CH-N-FML #07798. DS: Adults. Reference: Ramallo & Cancino (2021).

Host *Lebias multidentata* (Jenyns) (syn. *Jenynsia multidentata*)
SI: Intestine. Lo: Medina River (26°83'S, 65°80'W) Tucumán Province. MD: CH-N-FML#07418, #07419. DS: Adults. Reference: Ramallo (2005b).

Host *Jenynsia alternimaculata* (Fowler) **
SI: Intestine. Lo: Isasmendi Stream (24°48'S, 64°26'W), Salta Province. MD: CH-N-FML # 7511. DS: Adults. Reference: Ailán-Choke *et al*. (2014). SI: Intestine. Lo: La Caldera River (24°35'S, 65°22'W) Salta Province. MD: UNSa-IEBI-I N°0053. DS: Adults. Reference: Present study. Remarks: New locality record.

Host *Odontesthes hatcheri* (Eigenmann) (syn. *Patagonina hatcheri*)
SI: Intestine. Lo: Alicurá Reservoir, Pellegrini Lake, Neuquén Province. MD: Not indicated. DS: Adults. Reference: Ortubay *et al*. (1994).

Host *Oncorhynchus mykiss* (Walbaum)
SI: intestine. Lo: Lezama Lake and Alicurá Reservoir, Neuquén Province. MD: Not indicated. DS: Adults and third- and fourth-stage larvae. Reference: Ortubay *et al*. (1994).

Host *Percichthys trucha* (Valenciennes)
SI: Intestine. Lo: Limay River, Río Negro-Neuquén Provinces. MD: Not indicated. DS: Adults. Reference: Szidat (1956).

Host *Trichomycterus spegazzinii* (Berg) ***
SI: Intestine. Lo: La Caldera River (24°35'S, 65°22'W) and Yacones River (24°40'S, 65°24'W), Salta Province. MD: CH-N-FML 07790. DS: Adults. Reference: Present study. Remarks: New host and locality records. Records: *Rhabdochona acuminata* has been recorded in many freshwater fishes from Patagonia and Northwest Argentina (Ortubay *et al*., 1994; Cremonte *et al*., 2002; Ramallo, 2005b; Cancino & Ramallo, 2008; Viozii *et al*., 2009; Ailán-Choke *et al*., 2014). Taking into account these records, this parasite is considered a widespread species, encompassing almost all of South America (Cremonte *et al*., 2002).

Rhabdochona fabianae **Ramallo, 2005**

Host *Bryconamericus iheringi* (Boulenger)
SI: Intestine. Lo: Medina River (26°83'S, 65°80'W), Tucumán Province. MD: (H) CH-N-FML # 07422; (A) CH-N-FML # 07423; (P) CH-N-FML # 07424. DS: Adults. Reference: Ramallo (2005b).

DISCUSSION

Parasites have been recognized as key components of the biodiversity of an ecosystem, regulating the abundance or density of host populations, stabilizing food webs, and structuring host communities (Luque, 2008; Luque *et al*., 2016). Despite these key roles, they remain an underestimated component of the total biodiversity in many regions of the planet (Luque *et al*., 2016). Thus, studies identifying hotspots of high parasite diversity, as well as areas of relatively low parasite diversity, are crucial for a complete understanding of the functioning of the biosphere (Luque & Poulin, 2007).

The present study constitutes the most complete list of nematode parasites of freshwater fish from Argentina, including a complete bibliographic search of research on the subject. However, our current knowledge of the diversity of the nematodes parasitizing freshwater fish in Argentina is far from complete, due to the lack of sampling in several hydrological basin, families, and species of freshwater fish. To date, most sampling have been done in Great River and Patagonian ichthyogeographic provinces, while fish in Andean Cuyan, Aymaran, and Pampean ichthyogeographic provinces (Cuyan and Pampean regions) have been scarcely studied. This study effort is probably associated to the development of this line of work in scientific research centers in these regions. To date, only a small fraction of freshwater fish families and species in Argentina have been examined (21 out of its 56 fish families and 65 out of its 570 fish species) for the presence records of nematode parasites (Mirande & Koerber, 2020). The highest number of nematode parasites reported in Siluriformes and Characiformes probably reflects sampling effort, since these fish orders have the highest number of species in Argentina (Mirande & Koerber, 2020). Moreover, many species belonging to the above-mentioned fish orders are commercialized, which makes them available for parasitologists. On the other hand, the high number of nematode species recorded on Galaxiiformes could be related with its abundance and widely distribution across Patagonia (Barriga *et al*., 2002; Baigun & Ferriz, 2003), which makes them available for parasitological surveys in this region (Brugni & Viozzi, 2008; Viozzi & Semenas, 2009; Viozzi *et al*., 2009; Fernandez *et al*., 2012, 2015). However, several fish taxa are poorly studied, such as Rivulidae, Poecillidae, Anablepidae (Cyprinodontiformes), and Cichlidae (Cichliformes) that also present a high richness species with respect to other fish orders recorded in Argentina (Mirande & Koerber, 2020). In addition, some endemic fish species, such as *Silvinichthys mendozensis* Arratia *et al*., *Trichomycterus heterodontus* Eigenmann, *T. belensis* Fernández & Vari, *Xyliphius barbatus* Alonso de Arámburu & Arámburu (Siluriformes), *Rhamphichthys hahni* (Meinken, 1937) (Gymnotiformes) (López *et al*., 2008), have not yet been examined for nematode parasites. Therefore, we recommend prioritizing the examination of previously mentioned fish species in further studies, which will allow elucidating the real pattern of distribution and host spectra of the nematode parasites of freshwater fish from Argentina.

Camallanidae harbored the highest number of nematode species recorded in freshwater fish from Argentina, with *S. hilarii*, *S. inopinatus* and *C. corderoi* as the most common adult nematodes recorded. These species present a wide range of phylogenetically distantly related

hosts belonging to different families of Characiformes and Siluriformes (in case of *S. hilarii* and *S. inopinatus*) and Atheriniformes, Galaxiiformes, Cyprinodontiformes, Centrarchiformes and Salmoniformes (in case of *C. corderoi*) (see Table 1). This fact could explain why these species are the most common, namely they are generalist species (see Moravec *et al*., 1993, 1997c; Ramallo, 1997, 2005a; Gallas *et al*., 2015; Rauque *et al.,* 2018; Ailán-Choke *et al*., 2020). On the other hand, helminth larvae exhibit a low host specificity in fish, which increases their chances of reaching the definitive host, which could explain the wide host range presented by *Contracaecum* sp. larvae (Esch *et al*., 1988). Rauque *et al*. (2018) also reported that *Contracaecum* sp. was also the most generalistic parasite, however due to the large size of salmonids, it is not likely that piscivorous birds consume adult fishes, so these fish hosts could represent a dead end for this parasite.

This checklist may contain errors derived from the inclusion of misidentified host species, such as *Astyanax bimaculatus*, *Leporinus maculatus*, *Serrasalmus spilopleura*, and *Zungaro zungaro*, since they are not distributed in Argentina according to Mirande & Koerber (2020). These last three host records were cited by Hamann (1984, 1986, 1995/1996, 1999), but the examined fishes were not deposited in a collection. Thus, these fish records are doubtful and it is difficult to assess its taxonomic identification. In the particular case of *A. bimaculatus*, it was cited by Cancino & Ramallo (2008), but according to Lucena & Soares (2016) the material identified as *A. bimaculatus* corresponds to *A. lacustris*. Problems in the identification and taxonomy of host may affect the reliability of any parasitological studies and has implications for the assessment of host specificity, the elucidation of relationship between parasite and host phylogenies and the establishment of trophic links illustrated by life-cycle studies (Naylor *et al*., 2012; Alves *et al.,* 2017). Therefore, it is recommendable that parasitologists deposit examined host in a reference collection and preserve a piece of host tissue in molecular-grade ethanol for sequencing and to work in synergy with fish taxonomists to be as accurate as possible in the fish identification (Alves *et al.,* 2017).

Other of obstacles that contribute to the lack of taxonomic accuracy in this checklist is the controversy about the validity of some nematode species that were previously listed. For instance, larvae of *Contracaecum rudolphi*, *Camallanus tridentatus,* and *Goezia* sp. are doubtful record of parasite and have to be carefully reviewed, since the examined material of these nematodes was not deposited in reference collections (Zeiss & Seigneur, 1981; Úbeda *et al*., 1989; Gilbert *et al*., 1993; Ortubay *et al*., 1994). It is important to highlight the need to clarify their taxonomic status by the examination of new material from type host and localities. Thus, our recommendation is the deposition of vouchers of the studied material in reference collections, and in the case of molecular studies the deposition of morphological voucher of molecular samples (*i. e*. piece of the organism used for the generation of molecular data, preserved in a way that can be used for morphological identification) (Blasco-Costa *et al.,* 2016).

Among the nematode taxa reported in Argentinian freshwater fishes, five were identified only to genus level. Most of them correspond to larval stages, such as *Eustrongylides* sp., *Contracaecum* sp., and *Hysterothylacium* sp. The accurate specific identification of larval stages of nematodes is problematic, because they lack key features that are present in adults only (Moravec, 1998). In addition, there are few studies dealing with their genetic characterization (for example Sardella *et al*., 2020). Another reliable way to determine the species is to obtain adult nematodes from experimental infections of the definitive hosts (Moravec, 1998). However, studies on life cycles of these parasites are scarce in Argentina (Brugni & Viozzi, 2009). Therefore, integrative studies combining morphological and molecular data are necessary to improve the taxonomic resolution of the unidentified nematode larvae and to elucidate the real patterns of diversity of nematodes in Argentinian freshwater fish.

When comparing the number of parasitic nematode species of Argentinian freshwater fishes with that in other countries of South America, such as Paraguay (González-Solís & Mariaux, 2011) and Brazil (Luque *et al*., 2011; freshwater records only), it turns out that Argentina has a low number of species. We conclude that the biodiversity of freshwater fish hosts and their nematode parasites in the country is underestimated, due to: 1) a small fraction of the potential freshwater fish host in Argentina have been examined for nematode parasites, 2) the sampling bias in certain geographic regions and host species that may not reflect the real distribution patterns of these parasites, and 3) the lack of accuracy in taxonomic identification of some nematode species and its host species. To fill this knowledge gap, it is necessary to perform further investigation on this group of parasites, expanding the number of fish species examined, especially in poorly studied geographical localities.

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Millipedes and centipedes (Myriapoda: Diplopoda, Chilopoda) in Swiss heated greenhouses, with seven species new for Switzerland

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Abstract: The international plant trade provides opportunities for the introduction of exotic species into tropical greenhouses around the world. The millipede and centipede fauna of greenhouses is barely known in Switzerland. We conducted a survey in greenhouses of nine botanical gardens and other institutions across Switzerland. We captured and identified 1390 individuals belonging to 14 millipede species and 43 individuals belonging to 9 centipede species. Most millipede individuals recorded (80.3%) were non-native as were the species (8/14). Most centipede individuals (55.3%) were non-native, but not the majority of the species (4/10). The species composition varied strongly among greenhouses with species originating from different parts of the world. Seven species already known from greenhouses in other European countries are reported for the first time in Switzerland. These are the millipedes *Cylindrodesmus hirsutus* Pocock, 1889, *Poratia obliterata* (Kraus, 1960), *Paraspirobolus lucifugus* (Gervais, 1836) and the centipedes *Mecistocephalus guildingii* Newport, 1843, *Tygarrup javanicus* Attems, 1929, *Lamyctes* (*Lamyctes*) *coeculus* (Brölemann, 1889b), and *Cryptops* (*Cryptops*) *doriae* Pocock, 1891. The relevance of these findings is discussed.

Keywords: Artificial habitats - botanical gardens - hothouses - invasive species - non-native species - passive dispersal - soil fauna - urban biodiversity.

INTRODUCTION

Millipedes (Diplopoda) and centipedes (Chilopoda) are two diverse groups of arthropods belonging to subphylum Myriapoda. Millipedes comprise around 11 000 described species worldwide (Enghoff *et al.*, 2015), while centipedes comprise around 3300 (Edgecombe & Giribet, 2007; Bonato & Zapparoli, 2011; Bonato *et al.*, 2016). In general, millipedes are mostly detritivores whilst centipedes are venomous predators. Myriapods are predominantly soil or ground-dwelling organisms but some species have adapted to other habitats and live in aerial parts of trees or show amphibious habits (Golovatch & Kime, 2009; Tsukamoto *et al.*, 2021). Millipedes and centipedes are usually found in humid and sheltered microenvironments in forests, mainly amongst leaf-litter, under tree bark or beneath stones (Golovatch & Kime, 2009; Voigtländer, 2011). However, some species are able to live in extreme environments such as deserts, high mountains, caves or littoral habitats (Demange, 1958; Barber, 2009a; Golovatch, 2009; Gobbi *et al.*, 2020). Millipedes and centipedes are present in all continents except Antarctica. Four of the five extant centipede orders (Scutigeromorpha, Lithobiomorpha, Geophilomorpha, and Scolopendromorpha) have very wide distributions, but the fifth one (Craterostigmomorpha) with only two known species, is only found in Tasmania and New Zealand (Bonato & Zapparoli, 2011). On the other hand, millipede orders tend to have smaller distribution ranges, making them a suitable group for biogeographical studies (Enghoff, 2015) and most millipede species have small distribution areas (Golovatch & Kime, 2009). Nevertheless, several millipede and centipede species have increased their distribution range by being transported by human means, settling in areas where they are not native and, in some cases, even becoming invasive (Stoev *et al.*, 2010).

International trade of cultivated plants and soil material allow the colonization of European plant nurseries and greenhouses, from where these species may have subsequently spread (Stoev *et al.*, 2010). In Europe, introduced myriapods seem to pose only a minor problem for the native biodiversity and human economic activities

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(Stoev *et al.,* 2010). Wittenberg (2005) agrees on this, but also states that the knowledge on introduced Myriapods in Switzerland is so scarce that no comprehensive list could be provided. However, some species such as the invasive *Oxidus gracilis* (C.L. Koch, 1847) have become a pest in several European countries (Stoev *et al.,* 2010; Gilgado, 2020) but their effect on native biodiversity has not yet been studied (Iniesta *et al.,* 2020). *Oxidus gracilis* was first reported in Switzerland by Bigler (1913) from greenhouses and it is currently the second most abundant inhabitant of urban private gardens in the city of Basel (Braschler *et al*., 2020).

Since heated greenhouses and plant nurseries are most likely hotspots for exotic myriapods in Europe, their examination is a prerequisite for the prevention of future invasions. These artificial environments provide a very special set of conditions such as higher and more stable temperature and humidity, and the presence of non-native plant species, compared to other synanthropic outdoor habitats in Europe (Decker *et al.,* 2014). Decker *et al.* (2014) provide an overview of the literature with millipede and centipede records in greenhouses of Europe, but since then several new findings have been reported (see for example Tuf *et al*., 2018; Dolejš *et al*., 2019; Damasiewicz & Leśniewska, 2020; Gregory & Lugg, 2020; Gregory, 2021). In Switzerland, the literature with greenhouse myriapods records is scarce (Bigler, 1913; Holzapfel, 1932; Pedroli-Christen, 1993; Golovatch *et al*., 2001a). Regarding millipedes, only four non-native species have been reported in Swiss greenhouses: *Amphitomeus attemsi* (Schubart, 1934), native to South America (Golovatch *et al*., 2001a); *Cylindroiulus truncorum* (Silvestri, 1896a), of Mediterranean origin (Holzapfel, 1932; Pedroli-Christen, 1993); *Oxidus gracilis*, an east Asian species (Bigler, 1913; Holzapfel, 1932; Pedroli-Christen, 1993); and *Poratia digitata* (Porat, 1889) of neotropical origin (Holzapfel, 1932; Pedroli-Christen, 1993). When the first records of *C. truncorum* and *O. gracilis* were made, they were limited to greenhouses (Bigler, 1913; Holzapfel, 1932; Pedroli-Christen, 1993), but they are currently widespread in other urban habitats in Switzerland (Vilisics *et al*., 2012; Braschler *et al*., 2020; Gilgado, 2020). Regarding centipedes, only four European native species, namely *Lithobius melanops* Newport, 1845, *Cryptops* (*Cryptops*) *hortensis* (Donovan, 1810), *Stenotaenia linearis* (C.L. Koch, 1835) and *Schendyla nemorensis* (C.L. Koch, 1837) have been reported from Swiss greenhouses (Holzapfel, 1932). These species live in the wild in Switzerland (Stöckli, 2009; Bonato *et al*., 2016).

In the present work we present an updated list of the millipede and centipede species inhabiting heated greenhouses of Switzerland and provide new records for seven non-native species.

MATERIAL AND METHODS

We were granted permission to sample in heated greenhouses of nine institutions across Switzerland (Table 1): the Botanical Garden of Basel University, Basel Zoo, Botanical Garden of the University of Bern, Conservatory and Botanical Garden of the City of Geneva, Botanical Garden of St. Gallen, Botanical Garden of the University of Fribourg, Botanical Garden of the University of Zurich, the Jurassica Botanical Garden (Porrentruy), and the Papiliorama Tropical Garden in Kerzers. The greenhouses were visited between June and December 2019. In each greenhouse two methods for invertebrate sampling were used: active search and pitfall trapping. At localities where more than one greenhouse was present (Porrentruy, Geneva, Zurich, and Fribourg), we used both sampling methods in the greenhouse that had the highest air temperature and humidity, and only applied active search in the other one. Active search was carried in each greenhouse by the same two members of the team (J.D.G and I.B.) for 30 minutes. We visually searched for millipedes and centipedes, which were captured with forceps and placed in vials with 70% ethanol. The active search targeted millipedes and centipedes on the ground, in leaf litter, under deadwood, stones, plates, pots, etc., and on the bark or plant stems. The pitfall consisted of plastic cups (5.8 cm in diameter each) half filled with propylene glycol and covered by a plastic plate to prevent water or leaves to fall in. We distributed eight pitfall traps throughout the soil area of the main greenhouse of each locality, hiding them as much as possible from the view of the visitors. The traps worked for seven days. Captured specimens were sorted in the lab and transferred to 70% ethanol.

Specimens were identified by J. D. Gilgado (Diplopoda) and D. Cabanillas (Chilopoda) by comparison of external morphology and/or sexual characters, by using keys of identification (Titova, 1981; Eason, 1982; Bonato *et al*., 2009, 2014; Mitić *et al*., 2012; Enghoff *et al*., 2013; Lewis, 2013) and the original descriptions or redescriptions of the species known to inhabit Switzerland (Pedroli-Christen, 1993; Stöckli, 2009; Gilgado 2020) or greenhouses of Europe (Kime & Enghoff, 2011, 2017; Decker *et al*., 2014). Specimens were prepared for long-term storage in ethanol and a voucher collection is deposited in the Naturhistorisches Museum Basel. Photos were taken using a KEYENCE VHX-6000 and a Panasonic Lumix DMC-FZ200 camera equipped with a Raynox DCR-250 macro lens.

TAXONOMIC PART

A total of 1390 individuals belonging to 14 millipede species and 47 individuals of 10 centipede species were identified (Table 2). Of them, 1116 millipede individuals (80.3%), belonging to 8 species (57.1%) and 26 centipede individuals (55.3%) belonging to 4 species (40%) were

Table 1. Names, location, and dates of visit of the greenhouses examined. The asterisk indicates additional active captures (not standardized).

Institution	Locality, Canton	Greenhouse	Code	Coordinates	Date 1	Date 2
Basel Zoo	Basel, Basel-Stadt	Altes Vogelhaus (Old bird house)	BZV	47°32'53.56"N, 7°34'43.13"E	3.10.19	10.10.19
Botanical Garden of St. Gallen	St. Gallen, St. Gallen	Tropischer Regenwald (Tropical rainforest)	SGR	47°26'24.12"N, 9°24'24.44"E	2.10.19	9.10.19
		Tropische Nutzpflanzen (Tropical cultures)*	SGN	47°26'24.50"N, 9°24'25.15"E	2.10.19	9.10.19
Botanical Garden of the University of Basel	Basel, Basel-Stadt	Tropenhaus (Tropical house)	BAT	47°33'31.06"N, 7°34'54.36"E	26.6.19	3.7.19
		Viktoriahaus (Victoria greenhouse)*	BAV	47°33'32.75"N, 7°34'54.06"E	20.03.19	
Botanical Garden of the University of Bern	Bern, Bern	Palmenhaus (Palm house)	BEP	46°57'8.99"N, 7°26'44.26"E	4.12.19	11.12.19
Botanical Garden of the University of Fribourg	Fribourg, Freiburg	Forêt tropicale (Tropical forest)	FRF	46°47'35.42"N, 7°9'18.17"E	23.10.19	30.10.19
		Plantes utiles tropicales (Tropical useful plants)*	FRP	46°47'33.70"N, 7°9'21.26"E	23.10.19	30.10.19
Botanical Garden of the University of Zurich	Zurich, Zurich	Tropischer Tieflandregenwald (Tropical lowland forest)	ZUT	47°21'28.45"N, 8°33'42.59"E	5.12.19	12.12.19
		Tropischer Bergwald (Tropical mountain forest)*	ZUB	47°21'28.49"N, 8°33'41.14"E	5.12.19	12.12.19
Conservatory and Botanical Garden of Geneva	Geneva, Geneva	Serre Tropicale Principale (Main Tropical Greenhouse)	GEP	46°13'31.44"N, 6°8'43.07"E	15.10.19	22.10.19
		Jardin d'hiver (Winter garden)*	GEH	46°13'33.61"N, 6°8'44.97"E	15.10.19	22.10.19
Jurassica Botanical Garden	Porrentruy, Jura	La Petite Serre Tropicale (The small tropical greenhouse)	JUP	47°24'48.78"N, 7°4'36.89"E	7.11.19	14.11.19
		La Grande Serre Tropicale (The large tropical greenhouse)*	JUG	47°24'48.88"N, 7°4'36.60"E	7.11.19	14.11.19
Papiliorama	Kerzers, Fribourg	Jungle Trek	PAP	46°59'24.05"N, 7°12'4.14"E	12.9.19	19.9.19

Table 2. Summary of the number of captured individuals of each species by greenhouse. An asterisk indicates that the species is a new record for Switzerland, (+) indicates that the locality was sampled during additional visual search. Abbreviations of the greenhouse names as in Table 1.

Class Diplopoda				**Locality (Institution/greenhouse)**															
Order **Family**	**Species**	**Origin**	**Total**	BZV	SG		BA			BE	FR		ZU		GE		JU		PAP
					SGR	SGN (+)	BAT	BAT (+)	BAV (+)		FRF	FRP (+)	ZUT	ZUB (+)	GEP	GEH (+)	JUP	JUG (+)	
Julida Blaniulidae	*Blaniulus guttulatus* (Fabricius, 1798)	Native	**98**	—	2	—	—	—	—	—	4	4	—	87	—	—	1	—	—
	Choneiulus palmatus (Němec, 1895)	Native	**81**	1	—	—	—	—	—	—	6	3	13	5	—	—	33	20	—
	Nopoiulus kochii (Gervais, 1847)	Native	**86**	—	—	—	—	—	—	—	—	—	7	42	1	—	30	6	—
Julida Julidae	*Cylindroiulus latestriatus* (Curtis, 1845)	Native	**2**	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
	Cylindroiulus salicivorus Verhoeff, 1908	Italy	**3**	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—
	Cylindroiulus truncorum (Silvestri, 1896a)	Mediterranean	**202**	6	—	6	1	—	—	7	—	—	11	12	135	22	—	2	—
Polydesmida Haplodesmidae	*Cylindrodesmus hirsutus* Pocock, 1889*	Indonesia or Melanesia	**317**	—	—	—	280	—	—	—	—	—	35	—	—	—	—	—	2
Polydesmida Oniscodesmidae	*Amphitomeus attemsi* (Schubart, 1934)	South America	**153**	3	—	10	—	—	—	5	17	2	43	1	49	10	3	10	—
Polydesmida Paradoxosomatidae	*Oxidus gracilis* (C.L.Koch, 1847)	East Asia	**362**	6	—	1	10	1	—	1	132	—	67	13	74	22	1	34	—
Polydesmida Polydesmidae	*Brachydesmus superus* Latzel, 1884	Native	**8**	—	—	—	—	—	—	—	—	8	—	—	—	—	—	—	—
	Propolydesmus testaceus (C.L.Koch, 1847)	Native	**1**	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Polydesmida Pyrgodesmidae	*Poratia digitata* (Porat, 1889)	Neotropical	**3**	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
	Poratia obliterata (Kraus, 1960)*	Neotropical	**9**	—	—	—	—	—	—	6	—	—	3	—	—	—	—	—	—
Spirobolida Spirobolellidae	*Paraspirobolus lucifugus* (Gervais, 1836)*	South America	**65**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	65

Table 2. Continued.

Class Chilopoda				Locality (Institution/greenhouse)															
Order **Family**	**Species**	**Origin**	**Total**	BZV	SG		BA			BE	FR		ZU		GE		JU		PAP
					SGR	SGN (+)	BAT	BAT (+)	BAV (+)		FRF	FRP (+)	ZUT	ZUB (+)	GEP	GEH (+)	JUP	JUG (+)	
Geophilomorpha Geophilidae	*Geophilus flavus* (De Geer, 1778)	Native	**1**	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Geophilomorpha Mecistocephalidae	*Mecistocephalus guildingii* Newport, 1843*	Amphi-atlantic	**11**	—	—	—	—	—	—	—	—	—	—	—	7	4	—	—	—
	Tygarrup javanicus Attems, 1929*	South Asia	**5**	—	—	1	—	—	—	—	—	—	—	—	—	2	—	1	1
Lithobiomorpha Henicopidae	*Lamyctes coeculus* (Brölemann, 1889)*	Unclear	**9**	—	—	—	—	—	—	—	—	3	1	—	5	—	—	—	—
Lithobiomorpha Lithobiidae	*Lithobius forficatus* (Linnaeus, 1758)	Native	**15**	—	—	—	—	2	—	3	—	—	—	—	4	—	6	—	—
	Lithobius melanops Newport, 1845	Native	**2**	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Scolopendromorpha Cryptopidae	*Cryptops anomalans* Newport, 1844	Native	**1**	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
	Cryptops doriae Pocock, 1891*	Palaeotropical	**1**	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
	Cryptops hortensis (Donovan, 1810)	Native	**1**	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
	Cryptops parisi Brölemann, 1920	Native	**1**	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—

non-native. This corresponds to 50% of the total number of species recorded and to 79.3% of the total number of individuals captured. Seven species are reported in Switzerland for the first time.

First records for the Swiss Fauna

Class Diplopoda de Blainville in Gervais, 1844
Order Polydesmida Pocock, 1887
Family Haplodesmidae Cook, 1895
Genus *Cylindrodesmus* Pocock, 1889
Cylindrodesmus hirsutus Pocock, 1889

Fig. 1

Material examined: NMB; 115 females, 9 juveniles; Switzerland, Basel-Stadt, Botanical Garden of the University of Basel, Tropenhaus, 47°33'31"N, 7°34'54"E, 270 m; 03.07.2019; J.D. Gilgado and I. Bobbitt leg. – 151 females, 5 juveniles; same data but in the collection of J.D.G. – NMB; 31 females, 2 juveniles; Switzerland, Zurich, Botanical Garden of the University of Zurich, Tropischer Tieflandregenwald, 47°21'28"N, 8°33'42"E, 438 m; 12.12.2019; J.D. Gilgado and I. Bobbitt leg. – 2 females; same data but in the collection of J.D.G. – NMB; 2 females; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59'24"N, 7°12'4"E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg.

Distribution: According to Recuero (2018), who compiled all the records of the species, it is currently a pantropical species appearing in many greenhouses in Europe (see also Dolejš *et al.*, 2019). It may be originally native to Indonesia or Melanesia (Golovatch *et al.*, 2001b).

Remarks: It is a small, white, or pinkish white species, with a hairy appearance. Some populations of this species include males (Read, 2008), but others are parthenogenetic and thus composed only by females (Golovatch *et al.*, 2000). All the individuals collected in Switzerland were females or juveniles. More detailed information about its morphology can be found in Read (2008), Golovatch *et al.* (2000) and Golovatch *et al.* (2001b).

Family Pyrgodesmidae Silvestri, 1896b
Genus *Poratia* Cook & Cook, 1894
Poratia obliterata (Kraus, 1960)

Fig. 2

Material examined: NMB; 1 subadult male, 2 females, 1 juvenile; Switzerland, Bern, Botanical Garden of the University of Bern, Palmenhaus, 46°57'9"N, 7°26'44"E, 520 m; 11.12.2019; J.D. Gilgado and I. Bobbitt leg. – 2 females; same data but in the collection of J.D.G. – NMB; 1 female; Switzerland, Zurich, Botanical Garden of the University of Zurich, Tropischer Tieflandregenwald, 47°21'28"N, 8°33'42"E, 438 m; 12.12.2019; J.D. Gilgado and I. Bobbitt leg. (Table 2). – 2 juveniles; same data but in the collection of J.D.G.

Fig. 1. Living specimen of *Cylindrodesmus hirsutus* from the Tropenhaus of the Botanical Garden of the University of Basel. Scale bar: 2 mm.

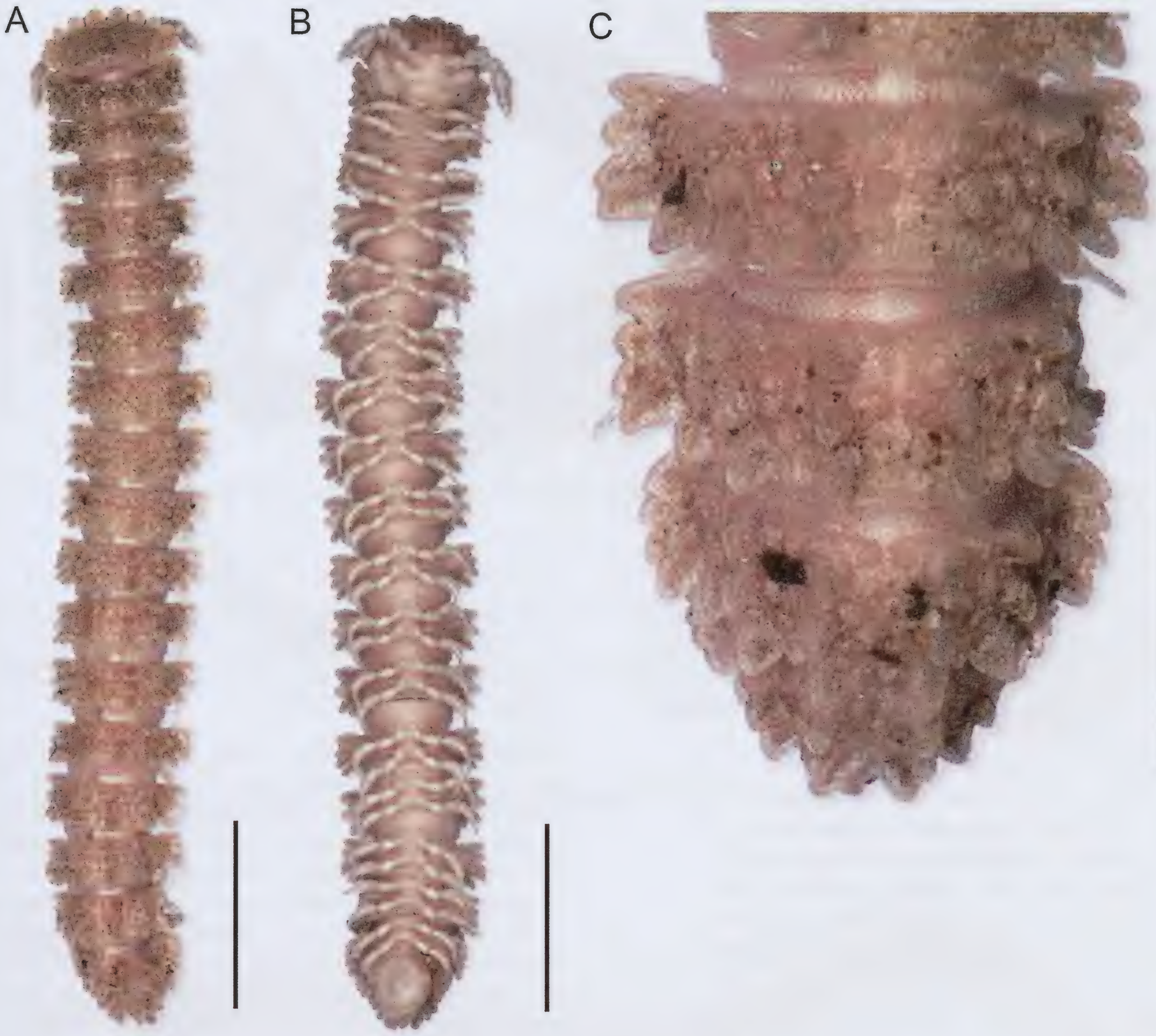

Fig. 2. *Poratia obliterata* from the Botanical Garden of the University of Bern. (A) Dorsal view. (B) Ventral view. (C) Detail of the last body rings. Scale bars: A, B, 1 mm; C, 0.5 mm.

Distribution: This species is found in the wild in Peru, Brazil and Colombia, and in Costa Rica (Golovatch & Sierwald, 2001). In Europe, the species has been recorded in greenhouses in Kiel, Germany (Wilck, 2000; Decker *et al*., 2014) and in Paris, France (Golovatch & Sierwald, 2001).

Remarks: It is very similar to *Poratia digitata*, also known in greenhouses of botanical gardens of Europe, but it can be distinguished by the number of rings (20 in *P. obliterata* and 19 in *P. digitata*) and the number of lateral lobulations in paraterga of ring 16-18(19) (always 4 in *P. obliterata* and mostly 3 in *P. digitata*) (Golovatch & Sierwald, 2001). All the individuals collected in Switzerland were females or juveniles.

Order Spirobolida Bollman, 1893
Family Spirobolellidae Brölemann, 1913
Genus *Paraspirobolus* Brölemann, 1902
***Paraspirobolus lucifugus* (Gervais, 1836)**
Fig. 3

Material examined: NMB; 17 males, 10 females, 7 juveniles; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59'24"N, 7°12'4"E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg. – 20 males, 11 females; same data but in the collection of J.D.G. (Table 2).

Distribution: This originally South American species has been found in greenhouses in England (Read, 2008), Denmark (Enghoff, 1975a) and Germany (Decker *et al*., 2014). In Germany, it was found in six different locations.

Fig. 3. *Paraspirobolus lucifugus* from the Papiliorama. (A) Adult female. (B) Adult male. (C) Gonopods. Scale bars: A, B, 2 mm; C, 0.5 mm.

Remarks: A description of the species can be found in Read (2008). Both males and females were collected in the present work. As a curiosity, this is one of the few known bioluminescent myriapods (Rosenberg & Meyer-Rochow 2009; Oba *et al.*, 2011).

Class Chilopoda Latreille, 1816
Order Geophilomorpha Pocock, 1896
Family Mecistocephalidae Bollman, 1893
Genus *Mecistocephalus* Newport, 1843
***Mecistocephalus guildingii* Newport, 1843**
Fig. 4

Material examined: NMB; 2 males, 4 females; Switzerland, Geneva, Conservatory and Botanical Garden of Geneva, Serre Tropicale Principale, 46°13'31"N, 6°8'43"E, 389 m; 22.10.2019; J.D. Gilgado and I. Bobbitt leg. – 1 male, 2 females, 2 juveniles; same data but in Jardin d'hiver, in the collection of D.C. (Table 2).

Distribution: *M. guildingii* is an amphi-Atlantic species that inhabits Atlantic islands and coastal or tropical mainland sites from the Americas to West Africa (Bonato *et al*., 2009). According to Bonato *et al*. (2009), *M. guildingii* is present in at least the Greater and Lesser Antilles, Bermuda Islands, Florida, Panama and Brazil in the Western Atlantic, but also in Madeira, the Cape Verde archipelago, Gambia, and Liberia in the Eastern Atlantic. Additionally, *M. guildingii* has been reported from coastal localities of the Pacific Ocean, specifically from Puerto Vallarta (Bonato *et al*., 2009) and the Botanical Garden of Culiacán Rosales in Mexico (López-Bonel *et al*., 2019). Zodinpuii *et al*. (2019) also reported *M. guildingii* from forests and cultivations of Mizoram in the northeast of India but this record seems highly uncertain and therefore needs verification. This species has been introduced to Europe, namely in France, Germany, and United Kingdom, where it is confined to hothouses (Latzel, 1895; Brölemann, 1930; Barber, 2008; Tillier, 2018).

Remarks: This species could be confused with *Mecistocephalus maxillaris* (Gervais, 1837) in European greenhouses. However, the two species can be distinguished by examining the proportion between the length of the areolate clypeus and the plagulae. In *M. guildingii*, the areolate clypeus is twice the length of the plagulae, whilst in *M. maxillaris* both structures are of the same length (Bonato *et al*., 2009). Both males and females of *M. guildingii* were detected in Swiss greenhouses.

Genus *Tygarrup* Chamberlin, 1914
***Tygarrup javanicus* Attems, 1929**
Fig. 5

Material examined: NMB; 1 female, 1 juvenile; Switzerland, Geneva, Conservatory and Botanical Garden of Geneva, Jardin d'hiver, 46°13'31"N, 6° 8'43"E, 389 m; 22.10.2019; J.D. Gilgado and I. Bobbitt leg. – 1 female; Switzerland, St. Gallen, Botanical Garden, Tropische Nutzpflanzen, 47°26'24"N, 9°24'24"E, 662 m; 09.10.2019; J.D. Gilgado and I. Bobbitt leg.; in the collection of D.C. – NMB; 1 female; Switzerland, Jura, Porrentruy, Jurassica Botanical Garden, La Grande Serre Tropicale, 47°24'48"N, 7°4'36"E; 430 m; 14.11.2019; J.D. Gilgado and I. Bobbitt leg. – NMB; 1 female; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59'24"N, 7°12'4"E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg. (Table 2).

Distribution: *Tygarrup javanicus* is probably native to southeastern Asia, originally described from the island of Java in Indonesia (Attems, 1929), with later

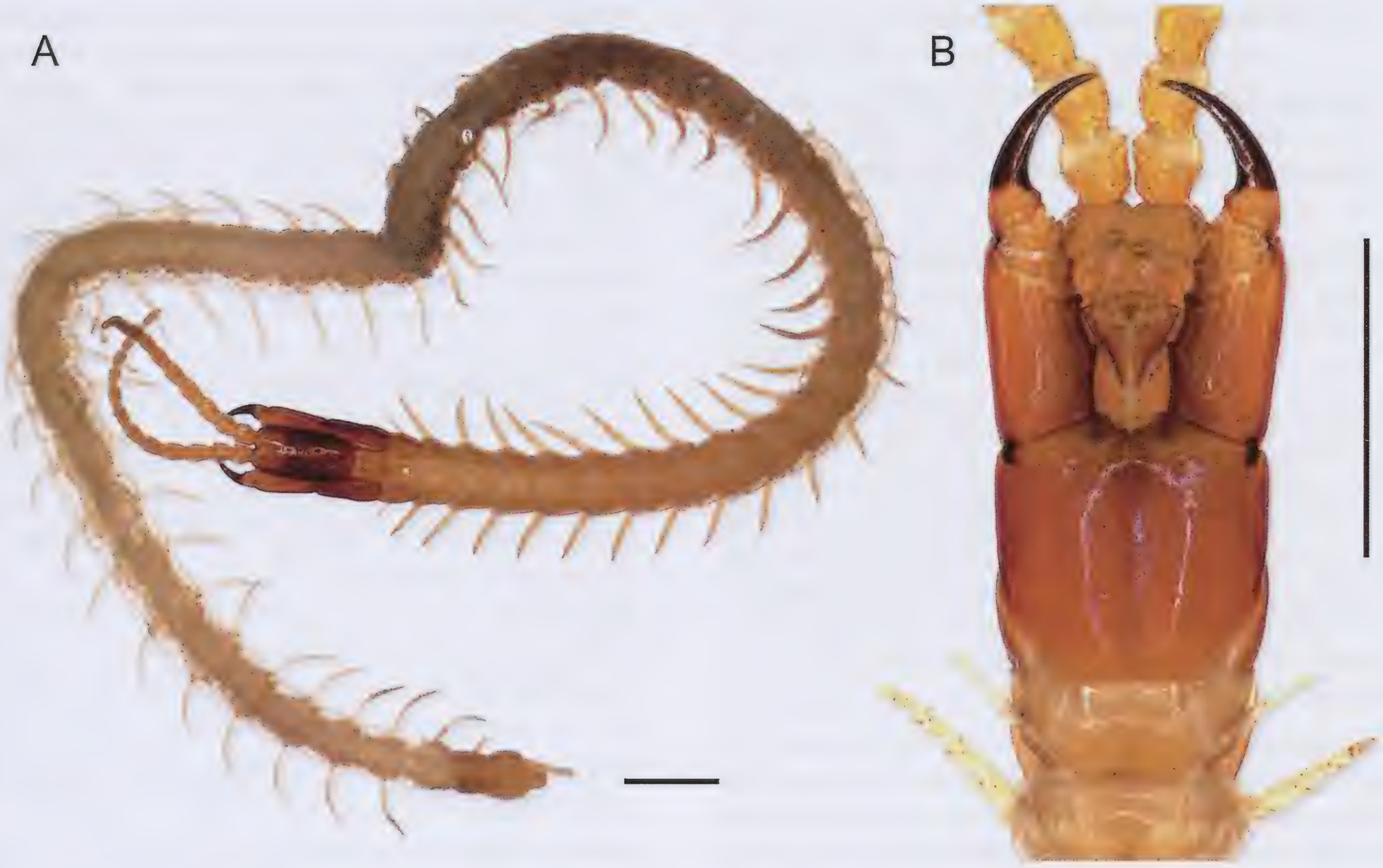

Fig. 4. *Mecistocephalus guildingii* from the Conservatory and Botanical Garden of Geneva. (A) Dorsal view. (B) Head in ventral view. Scale bars: 1 mm.

Fig. 5. *Tygarrup javanicus* from the Papiliorama, Kerzers. Dorsal view. Scale bar: 1 mm.

records in the Seychelles, Cambodia, Vietnam, and Mauritius (Demange, 1981; Titova, 1981; Bonato & Minelli, 2010). This species was presumably introduced to the Hawaiian islands (Bonato *et al*., 2004) and also to Europe. The species has been recorded in Austria, Czech Republic, Germany, Poland, Russia, Slovakia, and United Kingdom, where it is only capable of living in heated greenhouses (Lewis & Rundle, 1988; Christian, 1996; Barber, 2009b, c; Decker *et al*., 2014; Tuf *et al*., 2018; Nefediev, 2019; Damasiewicz & Leśniewska, 2020).

Remarks: Complete data about its morphology can be consulted in Bonato *et al*. (2004). All adult specimens from Swiss greenhouses were sexed as females.

Order Lithobiomorpha Pocock, 1895
Family Henicopidae Pocock, 1901
Genus *Lamyctes* Meinert, 1868
Subgenus *Lamyctes* Meinert, 1868
***Lamyctes* (*Lamyctes*) *coeculus* (Brölemann, 1889b)**
Fig. 6

Material examined: NMB; 1 female; Switzerland, Zurich, Botanical Garden of the University of Zurich, Tropischer Tieflandregenwald, 47°21'28"N, 8°33'42"E, 438 m; 12.12.2019; J.D. Gilgado and I. Bobbitt leg. – NMB; 2 females, 1 juvenile; Switzerland, Fribourg, Botanical Garden of the University of Fribourg, Plantes utiles tropicales, 46°47'35"N, 7°9'18"E; 631 m; 30.10.2019; J.D. Gilgado and I. Bobbitt leg. – NMB; 3 females; Switzerland, Geneva, Conservatory and Botanical Garden of Geneva, Serre Tropicale Principale, 46°13'31"N, 6°8'43"E, 389 m; 22.10.2019; J.D. Gilgado and I. Bobbitt leg. – 2 females; same data but in the collection of D.C. (Table 2).

Distribution: The family Henicopidae is native to the Southern Hemisphere, although the origin of *L. coeculus* is uncertain. This species was first detected in a greenhouse in Italy (Brölemann, 1889a) and subsequently reported from greenhouses in Sweden, France, Illinois (U.S.A.), Finland, Denmark, United Kingdom, Germany, and the Asian part of Russia (Lohmander, 1923; Brölemann, 1930; Auerbach, 1952; Lehtinen, 1960; Enghoff, 1975b; Barber, 2009c; Decker *et al*., 2014; Nefediev *et al*., 2016). This species has been recently recorded in new greenhouses of France (Tillier, 2018) and the United Kingdom (Gregory & Lugg, 2020). *Lamyctes coeculus* has been reported outdoor in Australia, Hawaii, the Galapagos Islands, Mexico, Argentina, Cuba, the Canary Islands, Democratic Republic of Congo, Tanzania, Madagascar, La Réunion and Palestine (Negrea *et al*., 1973; Enghoff, 1975b; Matic *et al*., 1977; Peck, 1990; Enghoff & Eason, 1992; Shear & Peck, 1992; Negrea & Matic, 1996; Zapparoli & Shelley, 2000; Edgecombe & Giribet, 2003; Edgecombe, 2004; Cupul-Magaña, 2011, 2015). It has been also recorded in Venezuela, but no collecting data were provided (Turk, 2009). Currently, this species could have a subcosmopolitan distribution and be widely extended all over the world, possibly due to anthropochory and thelytoky (Enghoff, 1975b; Edgecombe & Giribet, 2003; Enghoff *et al*., 2013).

Remarks: Worth mentioning another blind henicopid species which could potentially inhabit European

Fig. 6. *Lamyctes coeculus* from the Conservatory and Botanical Garden of Geneva. (A) Dorsal view. (B) Lateral view of head and first segments of trunk. Scale bars: A, 1 mm; B, 0.5 mm.

greenhouses and be confused with *L. coeculus* (Enghoff *et al*., 2013): *Lamyctes* (*Lamyctes*) *hellyeri* Edgecombe & Giribet, 2003, which differs in having a higher number of antennal articles (29-33 vs. 24 in *L. coeculus*) and the presence of a distal spinose projection on the tibiae of legs 12 (Edgecombe & Giribet, 2003). All examined specimens of *L. coeculus* from Swiss greenhouses were sexed as females.

Order Scolopendromorpha Pocock, 1895
Family Cryptopidae Kohlrausch, 1881
Genus *Cryptops* Leach, 1814
Subgenus *Cryptops* Leach, 1814
***Cryptops* (*Cryptops*) *doriae* Pocock, 1891**
Fig. 7

Material examined: NMB; 1 juvenile; Switzerland, Fribourg, Kerzers, Papiliorama, Jungle Trek, 46°59'24"N, 7°12'4"E, 438 m; 19.09.2019; Gilgado and I. Bobbitt leg. (Table 2).

Distribution: *Cryptops doriae* is natively found in tropical areas of Asia and Australia, namely in the Seychelles, Kazakhstan, Uzbekistan, Nepal, India, Burma, Laos, Vietnam, Cambodia, Philippines, Pahang (Malaysia), Sumatra and Java (Indonesia), Tonga, and Papua New Guinea (Pocock, 1891; Silvestri, 1894a; Attems, 1907, 1938; Lewis, 1999, 2007a, 2010; Schileyko, 2001, 2007; Schileyko & Stoev, 2016; Khanna, 2008; Nguyen *et al*., 2019; Dyachkov, 2020; Dyachkov & Nedoev, 2021). Additionally, *C. doriae* has been detected in European greenhouses in the United Kingdom (Lewis, 2007b) and in Germany (Decker *et al*., 2014).

Remarks: *Cryptops doriae* can be readily distinguished from native species by the presence of one or two saw teeth on the ventral surface of the femora of the ultimate leg pair. The morphology of the species has been studied in depth by Lewis (2009, 2013).

DISCUSSION

With some variation among greenhouses, millipedes were generally much more abundant (1390 individuals) than centipedes (47 individuals). Despite the differences in abundance, the number of centipede species (10) was not much lower than that of millipedes (14), as few millipede species had very high abundances (Table 2). The reason for the higher abundance of millipedes may be related to their trophic level. Millipedes are mostly detritivores consuming decaying leaf litter (David, 2015), a frequently occurring resource in greenhouses. Centipedes are predators (Voigtländer, 2011) and their populations depend, among others, on the abundance of prey. Centipedes are also rapid runners often escaping the forceps of the samplers. However, this may not explain the difference of the 30 times higher abundance of millipedes.

The high numbers of non-native millipede and centipede species found are remarkable. Interestingly, seven of these species have not previously been recorded in Switzerland. However, their presence in greenhouses in Switzerland was expected, as these species were already

Fig. 7. *Cryptops doriae* from the Papiliorama. Dorsal view. Scale bar: 2 mm.

found in greenhouses of other European countries (see for example Decker *et al*., 2014). In addition to the comments made on the new records, it is also worth mentioning the millipede *Cylindroiulus salicivorus* Verhoeff, 1908 (Table 2), an Italian species that is spreading outdoors across Europe (Read *et al*., 2002; Lee, 2006; Spelda, 2005; Kime & Enghoff, 2017) and has been only recently recorded in Switzerland from two urban private gardens in Basel (Gilgado, 2020). Conversely, the non-native centipede species found in the present work, *M. guildingii*, *T. javanicus*, *L. coeculus* and *C. doriae,* have never been never reported outdoors in Europe, most probably because they may not be able to survive in temperate climates.

There is increasing literature on non-native myriapods found in greenhouses in Europe (see for example Dányi & Tuf, 2016; Tuf *et al*., 2018; Dolejš *et al*., 2019; Damasiewicz & Leśniewska, 2020; Gregory, 2021). However, there are few comprehensive species lists for countries, an exception being Decker *et al*. (2014) for Germany. These authors used data from 46 greenhouses and re-surveyed 29 of them. Despite the higher number of greenhouses examined, Decker *et al.* (2014) reported a similar percentage of non-native species from different continents (34%) as found in our study (41.7%; Table 2). Most of the myriapod species found in Swiss greenhouses are also present in greenhouses in Germany. However, some native Western European species found in Swiss greenhouses were not recorded in German greenhouses, such as *Propolydesmus testaceus* (C.L. Koch, 1847), *Cryptops* (*Cryptops*) *anomalans* Newport, 1844 and *Cryptops* (*Cryptops*) *parisi* Brölemann, 1920, as well as some non-native species such as *C. salicivorus* (in Germany only known from parks or gardens) or *M. guildingii*. On the other hand, Decker *et al*. (2014) reported 10 non-native myriapoda species in German greenhouses that were not found in the present study. The apparent absence of these species in Switzerland might be due to the lower number of greenhouses examined, although preventive measures taken by some institutions, use of pesticides, or presence of predators such as birds, may also reduce the number of introduced species.

The results on millipedes and centipedes indicate that despite greenhouses harbouring a mix of native and non-native species, the latter are predominant. Native centipedes from this study are mostly eurioic species able to colonise and exploit new habitats. Amongst them, *L. forficatus* (Linnaeus, 1758), *L. melanops* and *C. hortensis* were previously recorded by Holzapfel (1932) in Swiss greenhouses and are also common in other European hothouses (Decker *et al*., 2014, Gregory & Lugg, 2020). The native millipedes recorded in our study are synanthropic species usually found in urban and suburban environments (Pedroli-Christen, 1993; Kime & Enghoff, 2011, 2017; Vilisics *et al*., 2012; Braschler *et al*., 2020). The non-native species found have various original distribution areas (Table 1), but those from tropical or subtropical areas are the most abundant, most probably favoured by the higher temperature and humidity in the greenhouses.

Several hypotheses have been proposed to explain the introduction and survival of alien centipedes in greenhouses, for example small body size that allows them to be passively transported with pot-plants and the presumable reproduction by thelytoky (Enghoff, 1975b; Golovatch, 2009; Stoev *et al*., 2010). These explanations could firmly support the presence and expansion of *L. coeculus* and *T. javanicus* throughout European greenhouses since they are small-sized species and only females have been ever detected in Europe (Enghoff, 1975b; Tuf *et al*., 2018). Other biological features such as high fertility, short development time and early maturity have been proposed to explain the ability of non-native millipedes and centipedes to survive in greenhouses (Golovatch, 2009; Tuf *et al*., 2018).

It is also possible that the absence of seasonal variations in environmental conditions negatively affects native millipede species in greenhouses, as some temperate species are adapted to seasonal variations in light, temperature and humidity in order to complete their life cycle (Fujiyama, 1996; David *et al*., 2003). Most of the non-native species coming from tropical areas have little potential to settle in the wild in Europe but some species from subtropical or temperate climates seem to spread into synanthropic habitats in Central Europe (Gilgado, 2020). This could be due to a lower number of competing species, absence of natural predators and parasites, etc. (Tilman, 1999). Thus, greenhouse managers should do their best to prevent the introduction of non-native soil-dwelling arthropods into their greenhouses and their later escape into the wild.

Regarding millipedes, the last comprehensive checklist for Switzerland made by Pedroli-Christen (1993) contains 127 taxa (125 species, two of them with two subspecies each), including those living indoors. Several new records have been made ever since: Bogyó *et al*. (2013) added *Polydesmus rupicursor* Verhoeff, 1907, Golovatch *et al*. (2001a) added *Amphitomeus attemsi*. Gilgado (2020) added *Cylindroiulus britannicus* (Verhoeff, 1891), *C. salicivorus*, *C. vulnerarius* (Berlese, 1888), *Heteroiulus intermedius* (Brölemann, 1892), *Anamastigona pulchella* (Silvestri, 1894b) and *Macrosternodesmus palicola* Brölemann, 1908. These records in the literature, added to the three new records in greenhouses reported in this study, result in a total of 136 millipede species for Switzerland. However, a revision is needed, because the validity of some of the species listed is discussed (Pedroli-Christen 1993). According to the checklist provided by Stöckli (2009), 62 centipede species have been reported from Switzerland (but precise data for two of them has not been published yet), although the author estimates that the number could reach 90 species for the country. The present study provides four new records for the Swiss

centipede fauna and adds seven species to the catalogue of centipedes able to live in Swiss greenhouses. Despite this progress, more centipede species could potentially be detected in further studies, for example *Polygonarea silvicola* Lawrence, 1955, *M. maxillaris*, *Pectiniunguis pauperatus* Silvestri, 1907 or *Lamyctes (Metalamyctes) africanus* (Porat, 1871), since they have been previously reported from other European greenhouses (Andersson *et al*., 2005; Stoev *et al*., 2010; Enghoff *et al*., 2013; Dányi & Tuf, 2016; Iorio, 2016).

In conclusion, our work provides the first comprehensive list of millipedes and centipedes in Swiss heated greenhouses (Table 2). Our results show a high share of non-native species from different regions of the world and provides seven new records for Switzerland. Not all exotic species reported in greenhouses of other European countries were found, probably because the small number of greenhouses examined and/or prevention measures taken in Swiss greenhouses. The present work suggests that the managers of these greenhouses should keep working on the prevention of introduction of exotic invertebrates.

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Supplement to the knowledge of the Scaphidiinae (Coleoptera: Staphylinidae) of the Moluccas

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Abstract: Newly studied collection of Moluccan Scaphisomatini comprise nine species described here as new: *Baeocera humicola* sp. nov., *Baeocera incurva* sp. nov., *Baeocera notata* sp. nov., *Baeocera paucivestis* sp. nov., *Baeocera punctigera* sp. nov., *Baeocera punctiventris* sp. nov., *Scaphisoma donati* sp. nov., *Scaphobaeocera plana* sp. nov., and *Scaphoxium lobatum* sp. nov. *Scaphisoma sublimbatum* Löbl, 1977 and *Scaphobaeocera schouteni* Löbl, 1980 are reported for the first time from the Moluccas. A new key to the Moluccan species of *Baeocera* is provided.

Keywords: Insecta - shining fungus beetles - taxonomy - distribution - Moluccas.

INTRODUCTION

Extensive collections of Moluccan Scaphidiinae, gathered by my friend Donat Agosti (Bern, Switzerland), were donated to the Muséum d'histoire naturelle, Genève. They were studied in part several years ago (Löbl, 2014). The present paper deals with the remaining specimens of these collections. The study yields 14 taxa new to sciences or to the Moluccan islands and thus raises the number of genera and species of scaphidiines known to occur there from three and 27 (Löbl, 2015a, 2021) to five and 41, respectively. All these species are members of the tribe Scaphisomatini. Notable is the absence of members of the nearly world-wide tribe Scaphidiini and of the pantropical Cypariini.

The first scaphidiines recorded from the Moluccan islands, two species of *Scaphisoma* Leach, 1815, have been collected a century ago on the island Buru and described as late as in the '70s (Löbl, 1976). Significant samples of Moluccan scaphidiines were obtained much later, by modern techniques and from several other islands. Nevertheless, it is still impossible to estimate the true richness of the group inhabiting the archipelago. The available modern material results from field work of only two entomologists, each disposing limited time for sampling. In addition, we still lack information about these myxomycetophagous and mycophagous rove beetles from a large number of Moluccan islands.

MATERIAL AND TECHNIQUES

The material studied is deposited in the collection of the Muséum d'histoire naturelle, Genève, Switzerland (MHNG). It was collected by sieving moist forest litter. The locality data of the type material are reproduced verbatim. All specimens are provided with appropriate identification labels.

The body-length is measured from the anterior pronotal margin to the posterior inner angles of elytra. The length/width of the mesepimera refer to their exposed part. The length/width ratios of the antennomeres are measured on slide-mounted antennae. Statements about abdominal microsculpture do not refer to the intersegmental membranes. The sides of the aedeagi refer to their morphological side with the ostium situated dorsally, while it is in resting position rotated 90°. The dissected body-parts are embedded in Euparal and fixed on a separate card on the same pin as the respective specimen. For primary references to all scaphidiines mentioned in the present paper see Löbl, 2018.

TAXONOMY

Baeocera Erichson, 1845

Remarks: Seven species of *Baeocera* are currently known from the Moluccas (Löbl, 2015a), while 12 have been reported from the Lesser Sunda, and 18 from New Guinea (Löbl, 2002, 2015b). Most of these species are members of the monophyletic *B. lenta* group. The present collection comprises six additional Moluccan species, all but one members of that group.

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Baeocera humicola sp. nov.

Figs 1-3

Materiel examined: *Holotype*; MHNG; male; MALUK: Kai Besar, Bombay, G. Dab, 3.IX.81, D. Agosti F911019.
Paratypes; MHNG; 3 females, with the same data as the holotype; – MHNG; 1 male; MALUK: Kai Besar, G. Tukrau nr Bombay, 4.IX.81, D. Agosti F91035.

Etymology: The species epithet is a noun meaning living in humus.

Diagnosis: The species is defined by the following characters in combination: Body-length about 1.20 mm, body blackish-brown; pronotum and elytra not microsculptured; lateral margins of pronotum and elytra separately arcuate, pronotum finely punctate; elytron entirely coarsely punctate, with basal stria extended to basal mid-width, sutural stria entire; hypomeron, mesanepisternum and mesepimeron impunctate; metaventrite and ventrite I coarsely punctate; ventrite I without basal wrinkles or striae; aedeagus symmetrical, with apical process abruptly narrowed near apex (lateral view), parameres hardly bent, nearly evenly broad, internal sac with complex sclerites, as in Fig. 3, lacking membranous scale or denticle-like structures.

Description: Length 1.18-1.20 mm, width 0.86-0.88 mm. Head and most of body blackish-brown, femora and tibiae lighter, reddish-brown, tarsi and antennae yellowish. Head with interocular distance about as dorsoventral eye diameter. Antennomere II about as long antennomere III. Length/width ratios of antennomeres as: III 23/5: IV 23/5: V 31/6: VI 29/6: VII 34/9: VIII 30/7: IX 37/11: X 37/13: XI 40/15. Pronotum and elytra separately arcuate. Pronotum not microsculptured, pronotal punctation hardly visible at 50 times magnification; lateral carinae of pronotum to part exposed in dorsal view. Point of scutellum exposed. Elytra nearly completely covering abdomen. Elytron weakly narrowed apically, with lateral margin rounded near base and apex, oblique in middle; lateral margin carinae concealed in dorsal view, adsutural area flat and narrow; sutural stria punctate, extended along base to form basal stria reaching basal mid-width; lateral stria punctate. Elytral disc not microsculptured, with punctation well delimited, much coarser than on pronotum, nearly regular, puncture intervals mostly two to three times puncture diameters. Hind wings fully developed. Hypomeron, mesanepisternum and mesepimeron impunctate. Mesoventrite punctate, without median ridge, fused with metaventral process. Mesepimeron about four times as long as wide and about three times as long as distance to coxa. Median part of metaventrite flattened, coarsely and densely punctate around smooth centre. Lateral area of metaventrite with punctation coarse and dense, denser than that on elytron; punctures well delimited, to part as large as puncture intervals, largest near anterior margin, evanescent near metacoxa. Submesocoxal lines parallel, with marginal punctures smaller than punctures on lateral area of metaventrite and not extended laterally along margin of metaventrite. Submesocoxal areas about 0.02 mm long, about as fourth of shortest interval to metacoxae. Metanepisternum flat, fused with metaventrite, its margin indicated by outer puncture row of metaventrite. Tibiae straight. Abdomen not microsculptured. Ventrite I about as coarsely and densely punctate as lateral area of metaventrite, basal punctures not enlarged and not elongate, not interrupted in middle, basal striae absent. Following ventrites finely punctate.
Male characters: Protarsomeres I to III hardly widened. Aedeagus (Figs 1-3) 0.32 mm long, weakly sclerotized, symmetrical. Apical process of median lobe gradually narrowed, with tip bent and acute in lateral view. Parameres hardly bent in both, dorsal and lateral, views and throughout nearly evenly wide. Internal sac with sclerotized complex as in Fig. 3, with long, apically widened flagellar guide-sclerite, lacking membranous scale- or denticle-like structures.

Habitat: Secondary forests on limestone, 200-400 m, litter from dead log and rotting leaves.

Distribution: Indonesia: Moluccas, Kai Besar Island.

Remarks: The species is a member of the *B. lenta* group. It falls in the key to the Moluccan species (Löbl, 2015a) to *B. vafra* Löbl, 2015. It may be distinguished by the parameres which are not widened and not bent apically, and by the bent tip of the apical process of the median lobe. In addition, the membranes of the internal sac of *B. vafra* bear denticle-like structures absent from *B. humicola*. The aedeagal characters of this new species suggest relationships with the New Guinean *B. papua* (Löbl, 1975) which may be readily distinguished by the ventrite I bearing basal wrinkles.

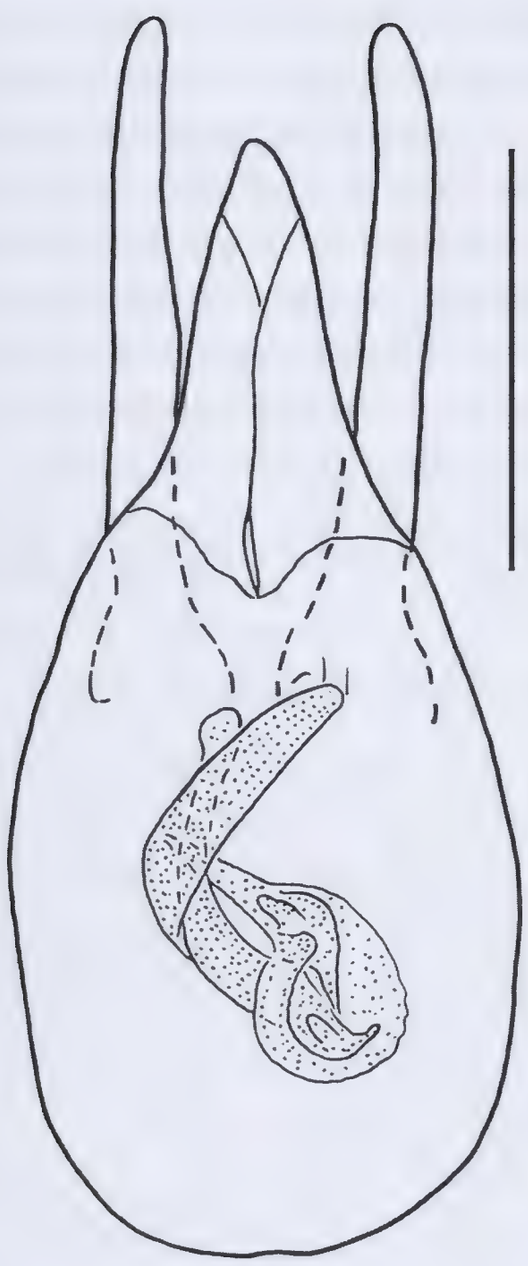
Baeocera incurva sp. nov.

Figs 4-6

Materiel examined: *Holotype*; MHNG; male; MALUK: Kai Besar, Bombay, G. Dab, 3.IX.81, D. Agosti F911019.
Paratypes; MHNG; 1 male, 2 ex. with the same data as the holotype. – MHNG; 2 males, 1 female; MALUK: Kai Besar, G. Tukrau nr. Bombay, 300-400 m, 7.IX.81 D. Agosti, F91075.

Etymology: The species epithet is a Latin adjective meaning bent.

Diagnosis: The species is defined by the following characters in combination: Body-length about 1.25-1.35 mm, body blackish with lighter apical abdominal segments; lateral margins of pronotum and elytra nearly



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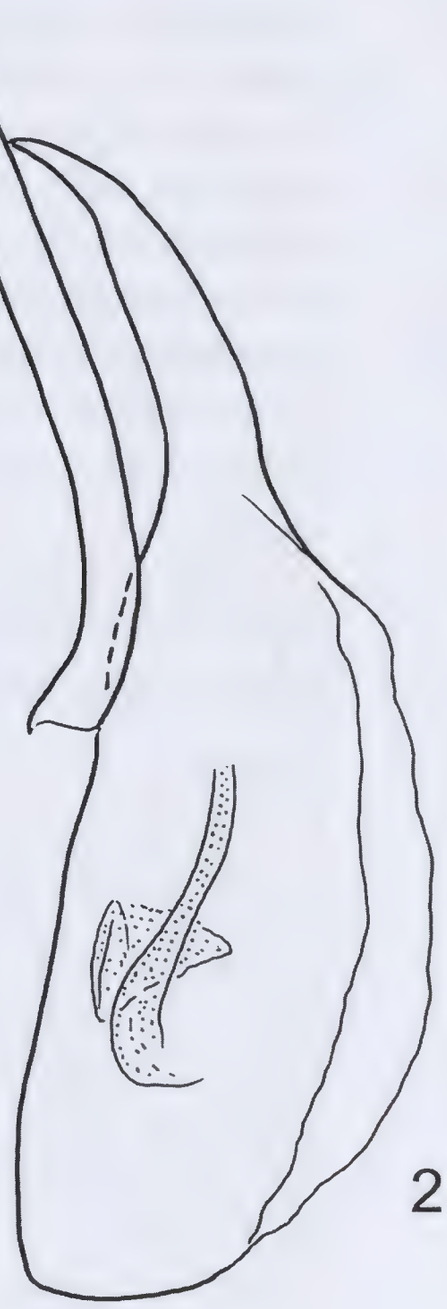

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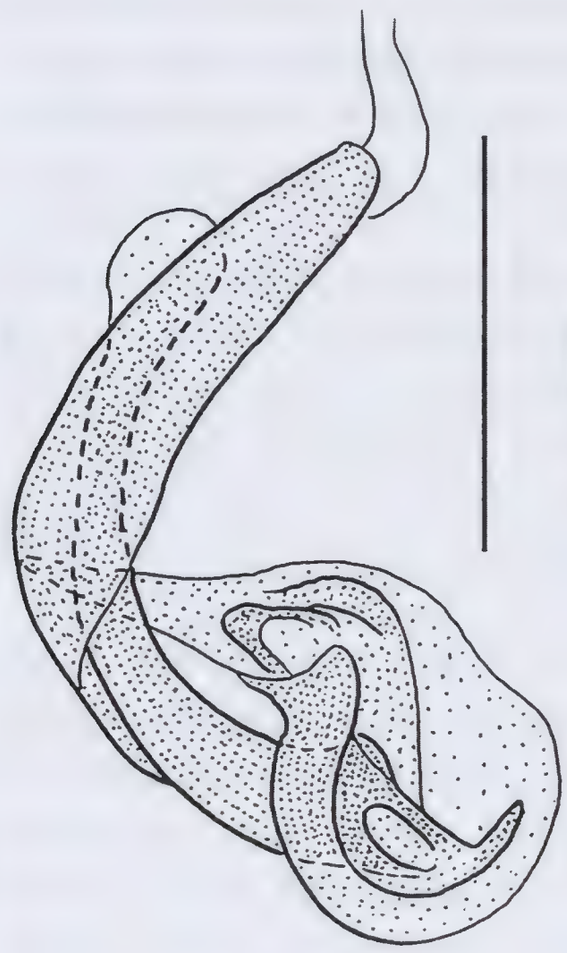

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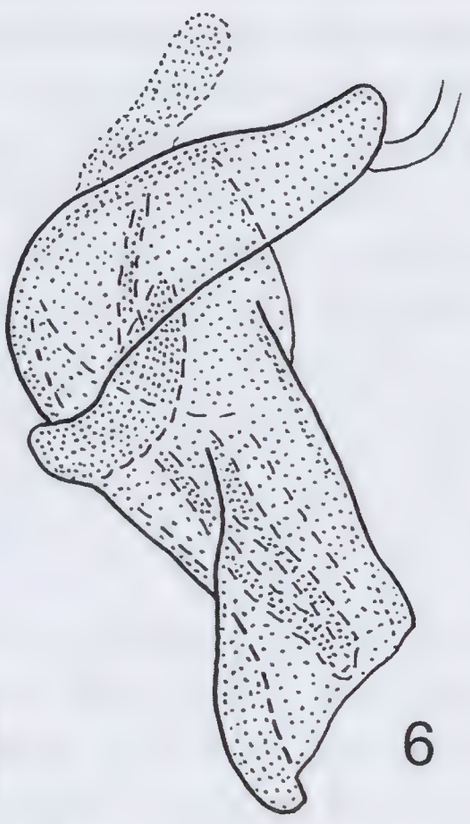

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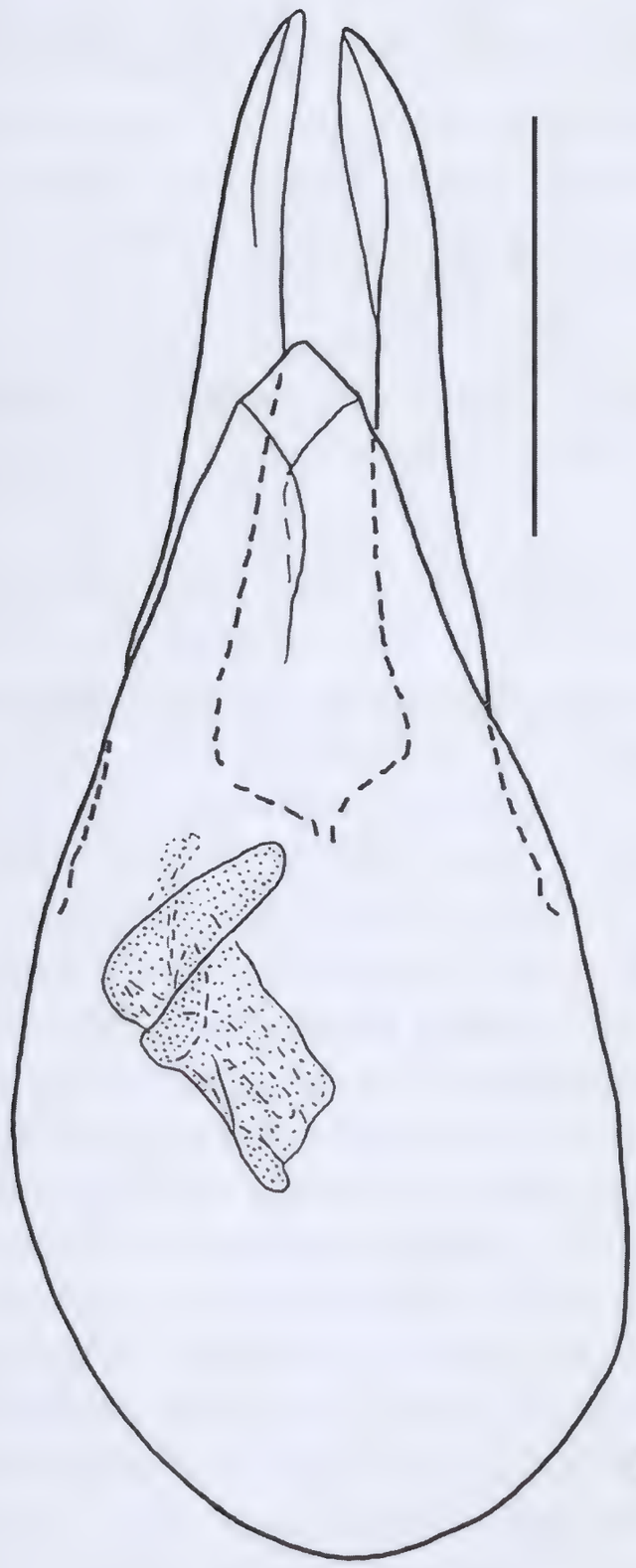

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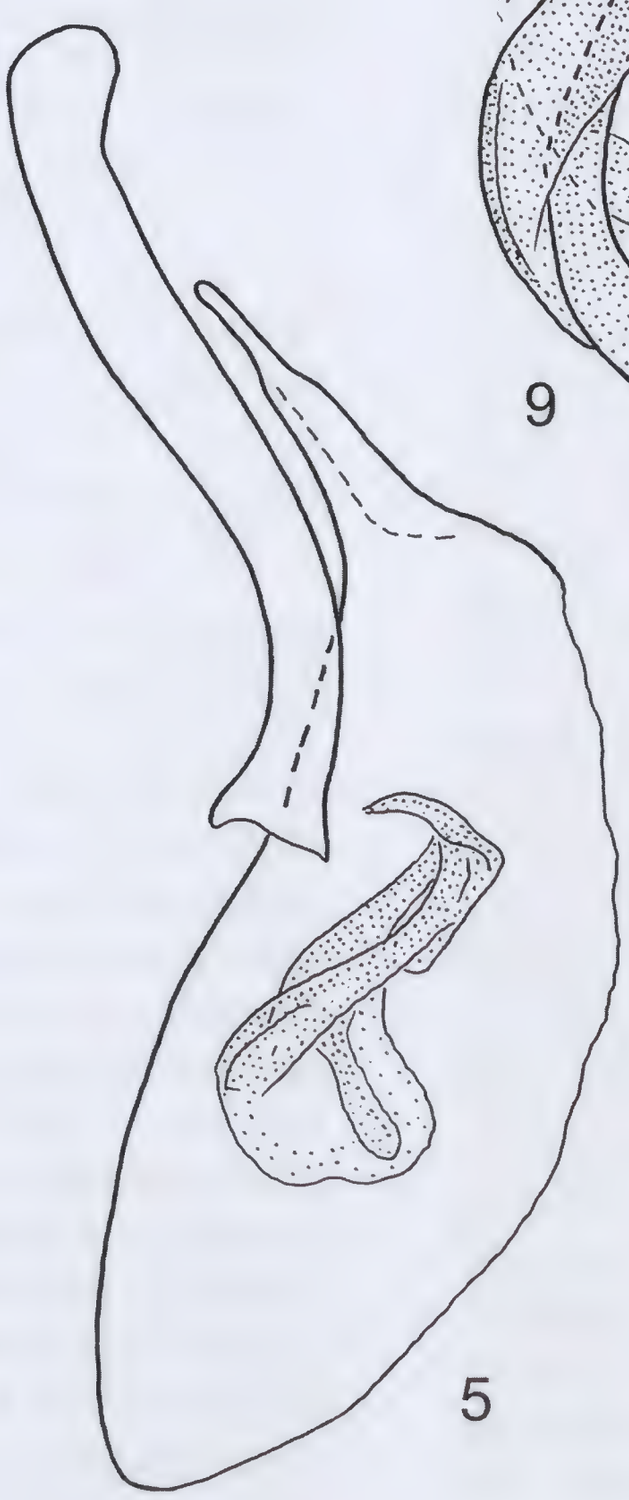

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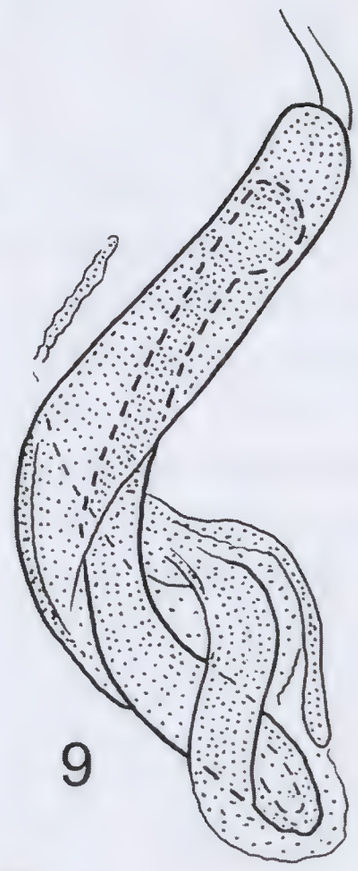

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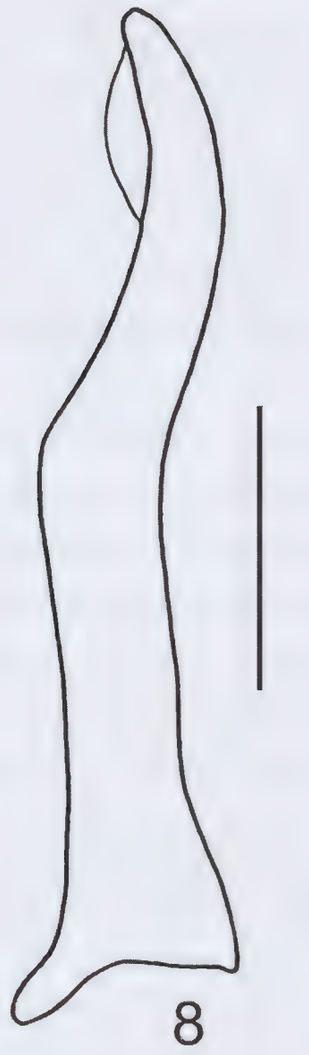

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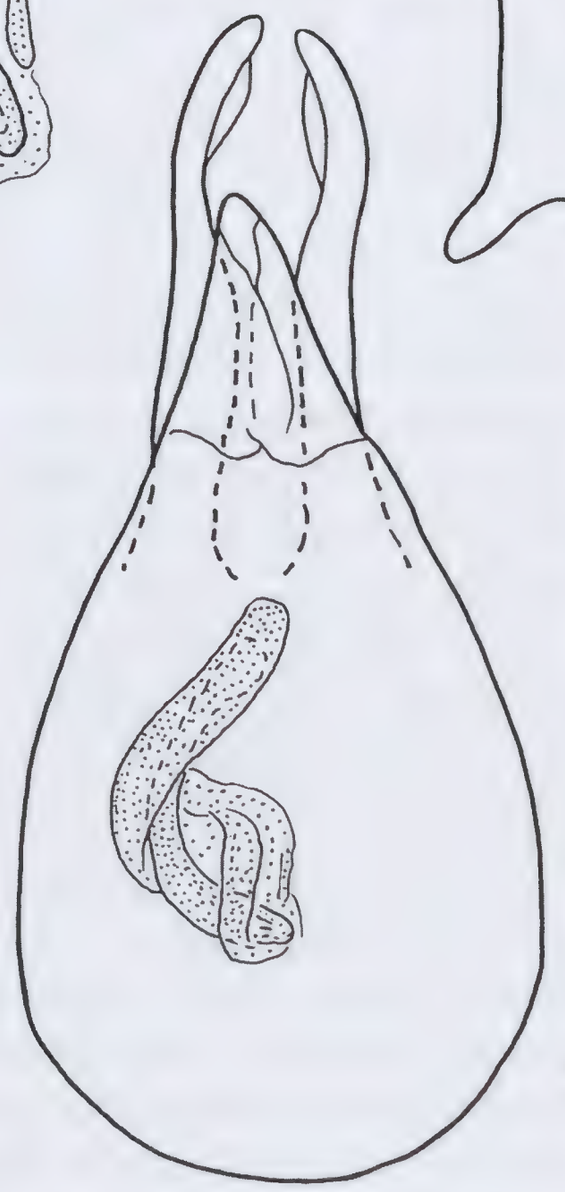

7

Figs 1-9. *Baeocera humicola* sp. nov. (1, 2) Aedeagus in dorsal and lateral views, scale bar = 0.1 mm. (3) Internal sac, scale bar = 0.05 mm. Figs 4-6. *Baeocera incurva* sp. nov. (4, 5) Aedeagus in dorsal and lateral views, scale bar = 0.1 mm. (6) Internal sac, scale bar = 0.05 mm. Figs 7-9. *Baeocera notata* sp. nov. (7) Aedeagus in dorsal view, scale bar = 0.1 mm. (8) Paramere in ventral view, scale = 0.05 mm. (9) Internal sac, scale = 0.05 mm.

continuously arcuate; pronotum finely punctate; elytron entirely coarsely punctate, lacking basal stria, sutural stria shortened, starting posterior of level of scutellum; hypomeron very finely punctate; mesepimeron, mesanepisterum, metaventrite and ventrite I distinctly punctate; ventrite I without basal wrinkles or striae; aedeagus symmetrical, with apical process in lateral view abruptly narrowed near apex, parameres sinuate, nearly evenly broad and bent dorsally in lateral view, internal sac with complex sclerites, as in Fig. 6, lacking membranous scale or denticle-like structures.

Description: Length 1.25-1.33 mm, width 0.85-0.88 mm. Head and most of body blackish, apical abdominal segments, femora and tibiae reddish-brown, tarsi and antennae yellowish. Head with interocular distance slightly larger than dorsoventral eye diameter. Antennomere II slightly longer than antennomere III. Length/width ratios of antennomeres as: III 24/6: IV 22/6: V 30/7: VI 30/7: VII 37/9: VIII 33/8: IX 41/12: X 41/14: XI 46/15. Pronotum and elytra nearly continuously arcuate. Pronotum not microsculptured, pronotal punctation hardly visible at 50 times magnification; lateral carinae of pronotum concealed in dorsal view. Point of scutellum exposed. Elytra nearly entirely covering abdomen. Elytron weakly narrowed apically, with lateral margin rounded; lateral margin carinae concealed in dorsal view, adsutural area flat and narrow; sutural stria punctate, shortened, starting well posterior of level of tip of scutellum; basal stria absent; lateral stria punctate. Elytral disc not microsculptured, with punctation well delimited, much coarser than on pronotum, nearly regular, puncture intervals mostly about as to three times puncture diameters. Hind wings fully developed. Impressed inferior part of hypomeron with few very fine punctures. Mesoventrite punctate, without median ridge, fused with metaventral process. Mesanepisternum pubescent, rather finely punctate. Mesepimeron punctate, about four times as long as wide and about three times as long as interval to coxa. Median part of metaventrite flattened, fairly coarsely, irregularly and densely punctate. Lateral area of metaventrite with punctation similar to that on elytron; punctures well delimited, clearly smaller than puncture intervals, evanescent near metacoxal margin. Submesocoxal lines slightly convex, with marginal punctures smaller than punctures on lateral area of metaventrite and not extended laterally along margin of metaventrite. Submesocoxal areas about 0.02-0.03 mm long, about as fifth of shortest interval to metacoxae. Metanepisternum flat, fused with metaventrite, its margin indicated by outer puncture row of metaventrite. Tibiae straight. Abdomen not microsculptured. Ventrite I about as coarsely and densely punctate as lateral area of metaventrite, basal punctures not enlarged and not elongate, basal wrinkles or striae absent. Following ventrites finely punctate.

Male characters: Protarsomeres I to III slightly widened. Aedeagus (Figs 4-6) 0.35-0.36 mm long, weakly sclerotized, symmetrical. Apical process abruptly narrowed near apex (lateral view), gradually narrowed in dorsal view. Parameres conspicuously sinuate, nearly evenly broad and bent dorsally in lateral view, hardly sinuate in dorsal view. Internal sac with complex sclerites as in Fig. 6, with very short flagellar guide-sclerite, lacking membranous scale- or denticle-like structures.

Habitat: Secondary forests on limestone, litter from dead log and rotting leaves.

Distribution: Indonesia: Moluccas, Kai Besar Island.

Remarks: The species is also member of the *B. lenta* group, as shown by its aedeagal characters. It falls in the key to the Moluccan species (Löbl, 2015a) to *B. vicina* Löbl, 2015. It may be easily distinguished from the latter as from other congeners by the shape of the parameres and by the internal sac possessing a short flagellum and reduced flagellar-guide sclerite. The New Guinean *B. praedicta* Löbl, 2002 possesses parameres rather similar to those of *B. incurva*. It differs notably in external characters, in particular by the not fused metanepisterna and the very finely punctate metaventrite.

Baeocera notata sp. nov.

Figs 7-10

Materiel examined: *Holotype*; MHNG; male; MALUC: Aru Isls: Kola Isl.: Watan, 27.8.81, D. Agosti F91936.
Paratype; MHNG; 1 female; MALUC: Aru Isl., Wokam, 22.8.81, D. Agosti F911970.

Etymology: The species epithet is a Latin adjective referring to the pronotum.

Diagnosis: The species is defined by the following characters in combination: Body-length about 1.35-1.45 mm, body dark brown; pronotum coarsely and densely punctate, with many punctures larger than puncture intervals; lateral margins of pronotum and elytra separately arcuate; elytron entirely coarsely punctate, with sutural stria shortened, lacking basal stria; hypomeron and mesanepisternum distinctly punctate; metaventrite and ventrite I coarsely punctate; ventrite I without basal striae or wrinkles; aedeagus symmetrical, with apical process narrowed apically, bent near tip in lateral view, apical halves of parameres bent and bearing subapical membranous lobe (dorsal view), widened posterior of basal third in lateral view, internal sac with complex sclerites as in Fig. 9, lacking membranous scale or denticle-like structures.

Description: Length 1.36-1.43 mm, width 0.90-1.0 mm. Head and body dark brown, femora and tibiae lighter, reddish-brown, tarsi and antennae yellowish.

Head with interocular distance slightly smaller than dorsoventral eye diameter. Antennomere II slightly longer than antennomere III. Length/width ratios of antennomeres as: III 28/7: IV 27/7: V 37/7: VI 35/7: VII 39/12: VIII 38/10: IX 39/12: X 37/14: XI 48/14. Pronotum and elytra separately arcuate. Pronotum not microsculptured, pronotal punctation conspicuously coarse and dense, distinct at 15 times magnification, consisting of sharply delimited punctures to part larger than puncture intervals; lateral carinae of pronotum hardly visible in dorsal view, bearing punctures very dense, larger than puncture intervals. Point of scutellum exposed. Elytra covering tip of abdomen, weakly narrowed apically, with lateral margins evenly, weakly rounded; adsutural area flat and narrow; sutural stria punctate, shortened, starting about 0.20 mm posterior of tip of scutellum; basal stria absent; lateral stria punctate. Elytral disc not microsculptured; punctation all over coarse and dense, punctures larger than those on pronotum but not as well delimited, puncture intervals mostly about as puncture diameters or slightly larger. Hind wings fully developed. Hypomeron not microsculptured, conspicuously punctate, with punctures about as large as pronotal punctures. Mesoventrite punctate, without median ridge, fused with metaventral process. Mesanepisternum conspicuously punctate, punctures similar to those on hypomeron. Mesepimeron impunctate, about four times as long as wide and three times as long as interval to coxa. Metaventrite flattened in middle, all over coarsely and densely punctate, smooth narrow apical band excepted; punctures on lateral part of metaventrite well delimited, to part as large or larger than puncture intervals. Submesocoxal lines slightly convex, with marginal punctures smaller than punctures on lateral area of metaventrite and somewhat extended laterally along margin of metaventrite. Submesocoxal areas about 0.03 mm long, as third of shortest interval to metacoxae. Metanepisternum flat, fused with metaventrite, its margin indicated by outer puncture row of metaventrite. Tibiae straight. Abdomen not microsculptured. Ventrite I densely and coarsely punctate, punctures smaller than those on lateral area of metaventrite, basal punctures not enlarged and not elongate, basal striae or wrinkles absent. Following ventrites finely punctate.

Male characters: Protarsomeres I to III slightly widened. Aedeagus (Figs 7-10) 0.37 mm long, weakly sclerotized, symmetrical. Apical process gradually narrowed apically, with tip bent and acute in lateral view. Parameres straight in basal halves, bent in apical halves, each with weakly sclerotized subapical lobe (dorsal view), narrow near bases and nearly evenly broad in apical two thirds, with slightly concave ventral margins (lateral view). Internal sac with complex sclerites, as in Fig. 9, with flagellar guide-sclerite widened apically, narrow accessory lateral sclerite present, lacking membranous scale- or denticle-like structures.

Habitat: Secondary/primary forest 5 km E of Mt. Sungai, shallow leaf litter, on limestone; understory with *Pandanus*.

Distribution: Indonesia: Moluccas, Aru Islands.

Remarks: The species is another member of the *B. lenta* group. It shares with the Moluccan *B. kaibesara* Löbl, 2014 and *B. vicina* Löbl, 2015, and the Papuan *B. praedicta* Löbl, 2002, elytra with shortened sutural striae. It may be readily distinguished from these three species by the hypomera and mesanepisterna conspicuously punctate. In addition, the shape of the parameres lobed subapically is diagnostic for this new species. Several species, such as the New Guinean *B. fortepunctata* Löbl, 2002 and the Philippine *B. hypomeralis* Löbl, 2012 also possess punctate hypomera but differs by the elytra having entire sutural striae and the impunctate or extremely finely punctate mesanepisterna. The Himalayan *B. cribrata* Löbl, 1992, shares the pronotum coarsely punctate, distinctly punctate hypomera and mesanepisterna, and elytra with shortened sutural striae. It may be easily distinguished by the punctation on lateral parts of the pronotum much coarser than that on pronotal centre.

Baeocera paucivestis sp. nov.

Figs 11-13

Materiel examined: *Holotype*; MHNG; male; MALUC: Tanimbar Isl., Yamdena, 22 km N Saumlaki, 11.IX.81, D. Agosti F911111.
Paratypes; MHNG; 1 male, 1 female MALUC: Tanimbar Isl., Yamdena, Bomaki, NW Saumlaki, 18.IX.81, D. Agosti F911148.

Etymology: The species epithet is a Latin adjective meaning poorly ornamented.

Diagnosis: The species is defined by the following characters in combination: Body-length about 1.20 mm, body light reddish-brown with darkened pronotum; lateral margins of pronotum and elytra separately arcuate; elytron entirely coarsely punctate, with uninterrupted basal stria joined to lateral stria, sutural stria not shortened; hypomeron and mesepimeron impunctate; mesanepisterum with hardly visible punctation; metaventrite and ventrite I fairly coarsely punctate; ventrite I without basal striae or wrinkles; aedeagus symmetrical, with apical process gradually narrowed apically, bent near tip (lateral view), parameres straight, nearly evenly broad, internal sac with complex sclerites as in Fig. 13, lacking membranous scale or denticle-like structures.

Description: Length 1.18-1.22 mm, width 0.83-0.85 mm. Head and body light reddish-brown, pronotum sometimes darkened. Femora as elytra, tibiae, tarsi and antennae yellowish. Head with interocular distance

about as dorsoventral eyes diameter. Antennomere II about 1.3 times as long as antennomere III. Length/width ratios of antennomeres as: III 22/7: IV 23/7: V 28/7: VI 24/7: VII 29/9: VIII 23/8: IX 30/12: X 30/13: XI 37/14. Pronotum and elytra separately arcuate. Pronotum not microsculptured, pronotal punctation hardly visible at 100 times magnification; lateral carinae of pronotum not visible in dorsal view. Point of scutellum exposed. Elytra nearly covering apex of abdomen. Elytron weakly narrowed apically, with lateral margin rounded near base and apex, oblique in middle; lateral margin carinae concealed or hardly visible in dorsal view, adsutural area flat and narrow; sutural stria punctate, not shortened, curved along pronotal lobe and extended to form basal stria; basal stria very shallow, uninterrupted, joined with lateral stria; lateral stria punctate. Elytral disc not microsculptured; punctation on humeral area very fine and similar to pronotal punctation, much coarser than that on pronotum on prevailing surface, nearly regular, punctures well delimited, puncture intervals mostly about two to three times puncture diameters. Hind wings fully developed. Hypomeron impunctate, with punctulate microsculpture. Mesoventrite punctate, without median ridge, fused with metaventral process. Mesanepisternum extremely finely punctate, punctures hardly visible at 100 times magnification. Mesepimeron impunctate, nearly four times as long as wide and nearly four times as long as interval to mesocoxa. Median part of metaventrite flattened, fairly finely and sparsely punctate. Lateral area of metaventrite with punctation coarse and very dense; punctures well delimited, to part as large or larger than puncture intervals, nearly touching metacoxal margin. Submesocoxal lines slightly convex, with marginal punctures smaller than punctures on lateral area of metaventrite and not extended laterally along margin of metaventrite. Submesocoxal areas about 0.03 mm long, as third of shortest interval to metacoxae. Metanepisternum flat, fused with metaventrite, its margin indicated by outer puncture row of metaventrite. Tibiae straight. Abdomen not microsculptured. Ventrite I very densely and rather finely punctate, punctures much smaller than those on lateral area of metaventrite, basal punctures not enlarged and not elongate, basal striae or wrinkles absent. Following ventrites very finely punctate.

Male characters: Protarsomeres I to III slightly widened. Aedeagus (Figs 11-13) 0.32 mm long, weakly sclerotized, symmetrical. Apical process gradually narrowed apically, with tip bent and acute in lateral view. Parameres straight, nearly evenly broad. Internal sac with complex sclerites, as in Fig. 13, with flagellar guide-sclerite widened apically, distinct accessory lateral sclerite, lacking membranous scale- or denticle-like structures.

Habitat: *Melaleuca* open forests on limestone, via Aram, Desa Lorulun; leave litter heavily infested with mycorrhiza, and rotten logs and primary forest at the northern end of the bay, in thick leave litter and rotting logs.

Distribution: Indonesia: Moluccas, Yamdena Island.

Remarks: The species is also member of the *B. lenta* group. It falls in the key to the Moluccan species (Löbl, 2015a) to *B. vafra* Löbl, 2015 and *B. variata* Löbl, 2015, but may be easily distinguished from them by the elytra having uninterrupted basal striae. The shape of the parameres and the internal sac are similar to those of *B. variata*. The Papuan *B. bacchusi* (Löbl, 1975) is similar in aedeagal characters and has also uninterrupted basal striae of the elytra. It may be readily distinguished from *B. paucivestis* by the body significantly smaller and black.

Baeocera punctigera sp. nov.

Figs 14-16

Materiel examined: *Holotype*; male; MHNG; MALUC: Tanimbar Isl., Kai Besar, G. Dab, 400 m, 5.IX.81, D. Agosti F911046.

Etymology: The species epithet is a Latin adjective meaning bearing punctures.

Diagnosis: The species is defined by the following characters in combination: Body-length about 1.2 mm long, body dark brown; pronotum coarsely and densely punctate, with many punctures larger than puncture intervals; lateral margins of pronotum and elytra separately arcuate; entire elytron coarsely punctate, sutural stria shortened, basal stria absent; mesepimeron with puncture row along anterior margin; hypomeron, mesanepisternum, metaventrite and ventrite I conspicuously punctate; ventrite I without basal striae or wrinkles; aedeagus symmetrical, with apical process narrowed apically, bent near tip (lateral view), parameres straight and evenly narrow in dorsal view, sinuate and widened toward apical third in lateral view, internal sac with complex sclerites as in Fig. 16, lacking membranous scale or denticle-like structures.

Description: Length 1.17 mm, width 0.80 mm. Head and body dark brown, femora and tibiae lighter, reddish-brown, tarsi and antennae yellowish. Head with interocular distance slightly larger than dorsoventral eye diameter. Antennomere II slightly longer than antennomere III. Length/width ratios of antennomeres as: III 28/7: IV 27/6: V 32/6: VI 28/6: VII 33/10: VIII 28/8: IX 35/13: X 35/14: XI 42/15. Pronotum and elytra separately arcuate. Pronotum not microsculptured, pronotal punctation conspicuously coarse and dense, distinct at 15 times magnification, consisting of sharply delimited punctures smaller than puncture intervals; lateral carinae of pronotum hardly visible in dorsal view, with punctures very dense, larger than puncture intervals. Point of scutellum exposed. Elytra covering

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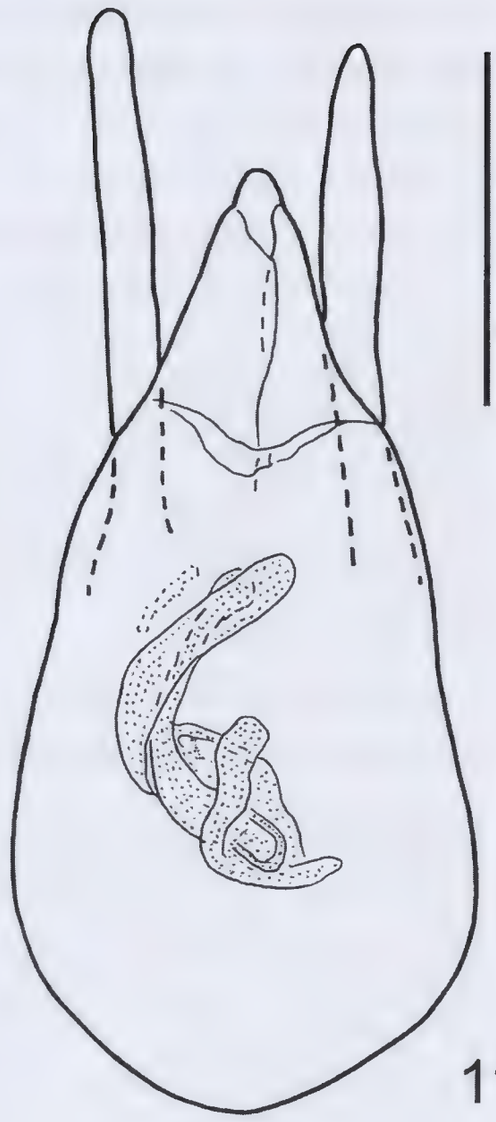
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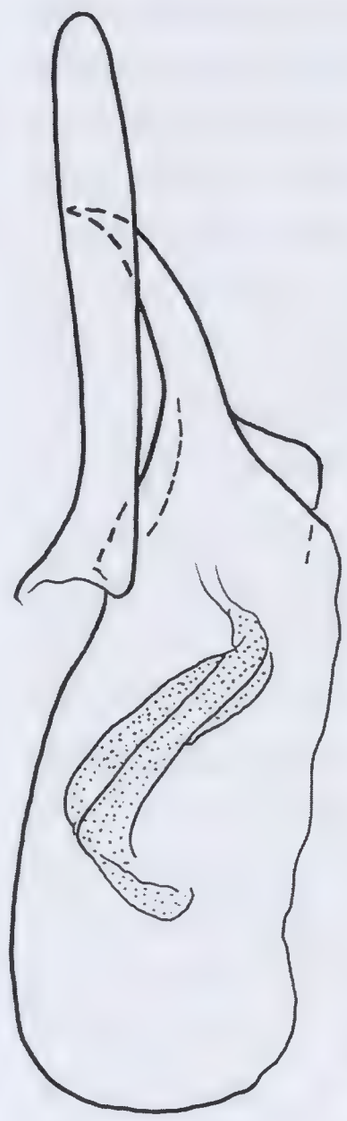
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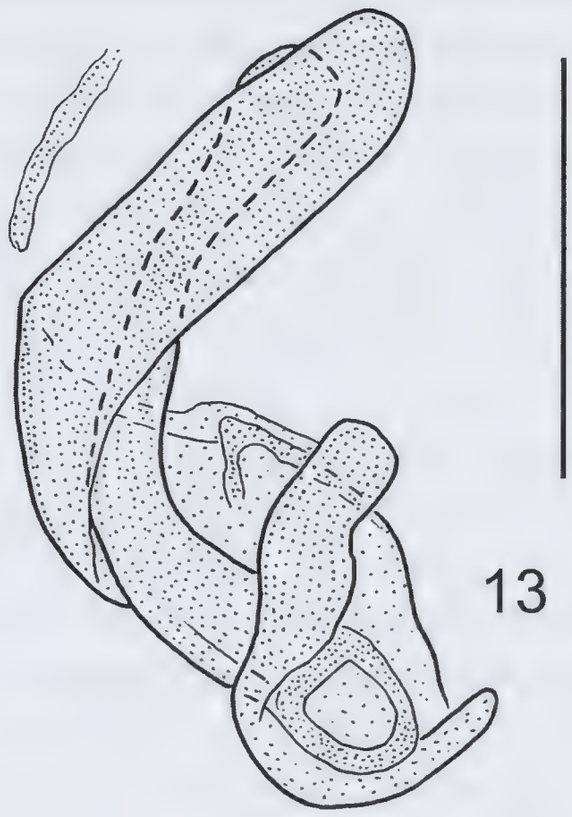
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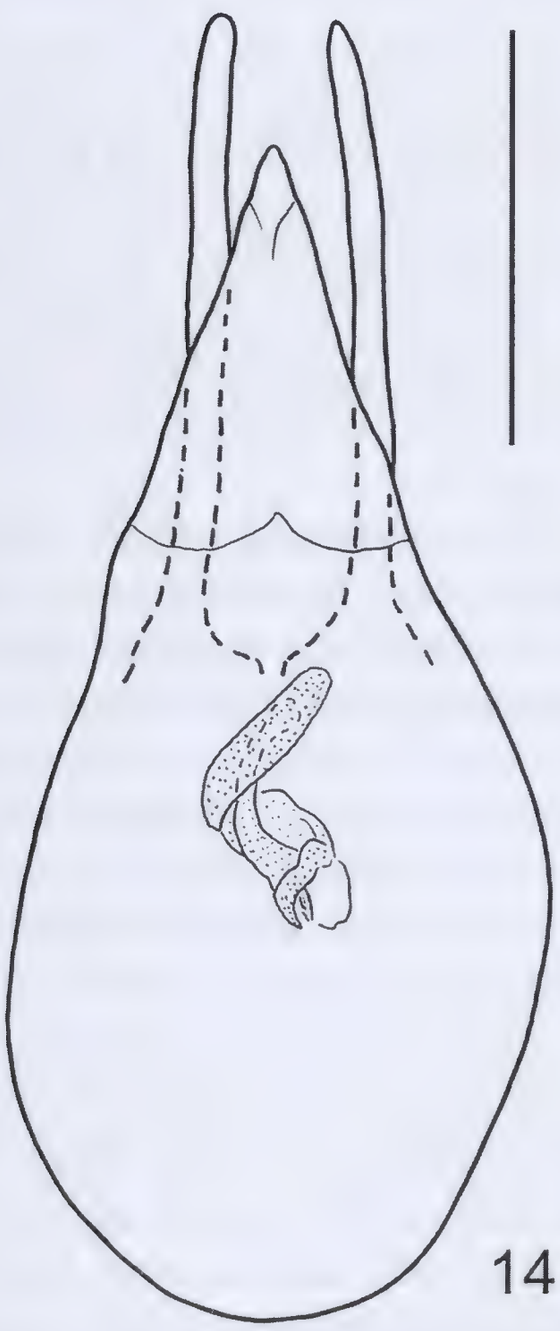
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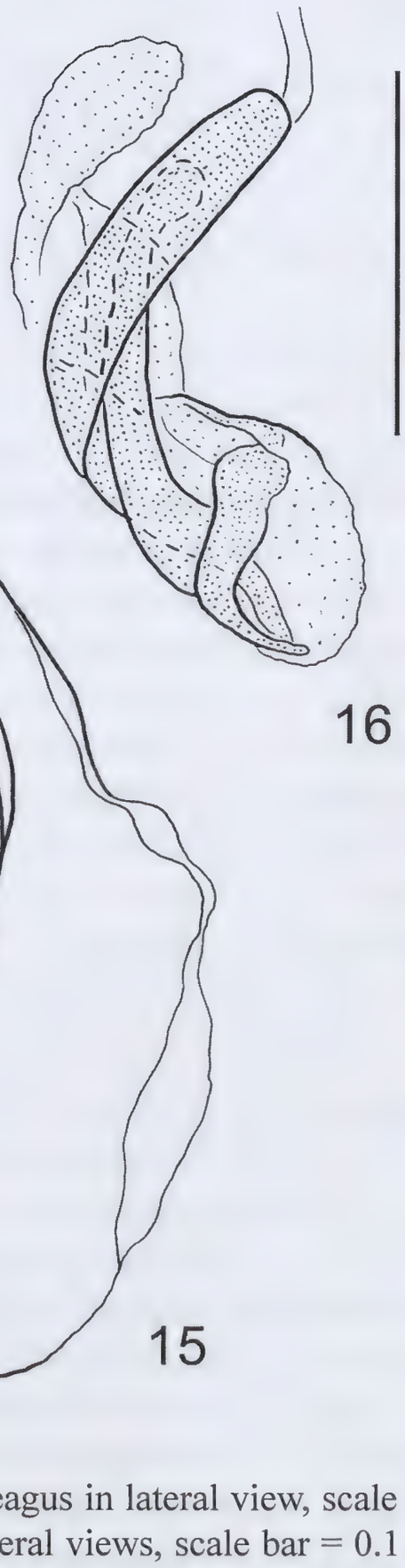
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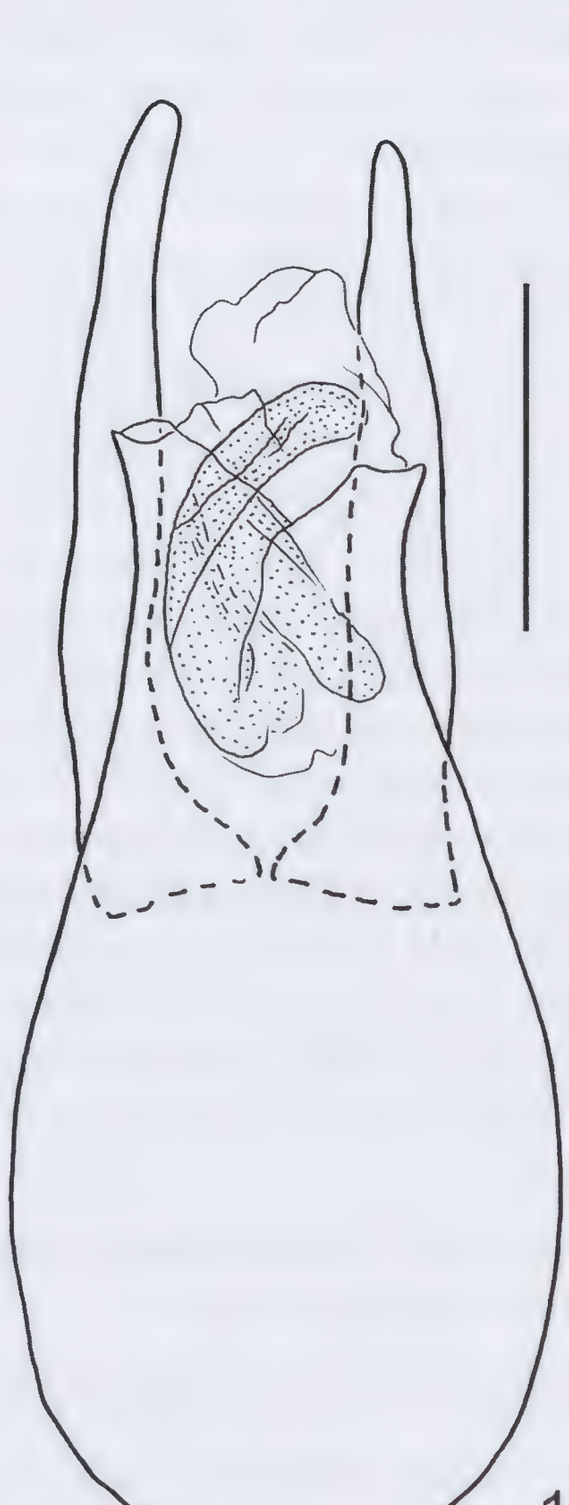
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Figs 10-18. *Baeocera notata* sp. nov. (10) Aedeagus in lateral view, scale bar = 0.1 mm. Figs 11-13. *Baeocera paucivestis* sp. nov. (11, 12) Aedeagus in dorsal and lateral views, scale bar = 0.1 mm. (13) Internal sac, scale bar = 0.05 mm. Figs 14-16. *Baeocera punctigera* sp. nov. (14, 15) Aedeagus in dorsal and lateral views, scale bar = 0.1 mm. (16) Internal sac, scale bar = 0.05 mm. Figs 17, 18. *Baeocera punctiventris* sp. nov. (17) Aedeagus in dorsal view, internal sac extruded, scale bar = 0.1 mm. (18) Paramere in dorsal view, scale bar = 0.05 mm.

abdomen, weakly narrowed apically, with lateral margins evenly, weakly rounded; adsutural area flat and narrow; sutural stria punctate, shortened, starting about 0.20 mm posterior of tip of scutellum; basal stria absent; lateral stria punctate. Elytral disc not microsculptured; punctation entirely coarse and dense, punctures larger than those on pronotum and nearly as well delimited, puncture intervals mostly larger than puncture diameters. Hind wings fully developed. Hypomeron not microsculptured, conspicuously punctate except on smooth areas along upper margin and near mesocoxa, with some punctures about as large as puncture intervals and as pronotal punctures. Mesoventrite punctate, without median ridge, fused with metaventral process. Mesanepisternum conspicuously punctate, punctures similar to those on hypomeron. Mesepimeron with row of coarse punctures along anterior margin, about three times as long as wide and three times as long as interval to coxa. Metaventrite flattened in middle, all over coarsely and densely punctate, narrow apical band excepted; punctures on lateral part of metaventrite well delimited, mostly larger than puncture intervals. Submesocoxal lines parallel, with marginal punctures smaller than punctures on lateral area of metaventrite and somewhat extended laterally along margin of metaventrite. Submesocoxal areas about 0.02 mm long, as fifth of shortest distance to metacoxae. Metanepisternum flat, fused with metaventrite, its margin indicated by outer puncture row of metaventrite. Tibiae straight. Abdomen not microsculptured. Ventrite I densely and coarsely punctate, punctures smaller than those on lateral area of metaventrite, basal punctures not enlarged and not elongate, basal striae or wrinkles absent. Following ventrites finely punctate.

Male characters: Protarsomeres I to III slightly widened. Aedeagus (Figs 14-16) 0.29 mm long, weakly sclerotized, symmetrical. Apical process gradually narrowed apically, with tip bent and blunt in lateral view. Parameres straight and evenly narrow in dorsal view, sinuate and gradually widened toward apical third in lateral view. Internal sac with complex sclerites, as in Fig. 16 with flagellar guide-sclerite widened apically, broad, nearly membranous accessory lateral sclerite, lacking membranous scale- or denticle-like structures.

Habitat: South slope of G. Dab, secondary forest on limestone, soil and very humid leaf litter.

Distribution: Indonesia: Moluccas, Tanimbar Islands.

Remarks: This is another species of the *B. lenta* group, in external characters very similar to *B. notata*. It may be easily distinguished from the latter by the mesepimeron bearing a row of coarse punctures along its anterior margin and by the aedeagal characters, in particular by the parameres straight and narrow in dorsal view. In addition, the body-size of *B. punctigera* is smaller, the antennae are shorter, with the antennomere XI less than 3 times as long as wide. While the aedeagus of *B. punctigera* is similar to that of the New Guinean *B. flagrans* Löbl, 2002, the species differs strongly from the latter by its external characters.

***Baeocera punctiventris* sp. nov.**

Figs 17-19

Materiel examined: *Holotype*; male; MHNG; MALUC: Tanimbar Isl., Kai Besar, G. Dab, 400 m 5.IX.81, D. Agosti F911046.
Paratype; MHNG; female; with the same data as the holotype.

Etymology: The species epithet is a Latin adjective meaning punctate ventrally.

Diagnosis: The species is defined by the following characters in combination: Body-length about 1.35-1.40 mm, body dark brown; lateral margins of pronotum and elytra nearly continuously arcuate; pronotum, elytra, hypomeron, mesanepisternum, lateral parts of metaventrite and ventrite I with similar, distinct punctation; elytron with sutural stria entire, basal stria present, broadly separated from lateral stria; mesepimeron punctate along anterior margin; ventrite I without basal striae or wrinkles; aedeagus symmetrical, with ventral side of apical process sinuate and bent at tip (lateral view), parameres nearly straight and slightly narrowed apically in dorsal view, evenly broad and weakly sinuate in lateral view, internal sac with complex sclerites, lacking membranous scale or denticle-like structures.

Description: Length 1.37-1.40 mm, width 0.95-0.97 mm. Head and body dark brown, femora and tibiae lighter, reddish-brown, tarsi and antennae lighter than tibiae, brown to yellowish. Head with interocular distance as dorsoventral eye diameter. Antennomere II hardly longer than antennomere III. Length/width ratios of antennomeres as: III 30/6: IV 33/6: V 46/7: VI 43/7: VII 51/9: VIII 40/8: IX 51/13: X 44/14: XI 48/14. Pronotum and elytra nearly continuously arcuate. Pronotum not microsculptured, pronotal punctation conspicuously dense and fairly coarse, barely distinct at 15 times magnification, consisting of sharply delimited punctures as large as and smaller than puncture intervals; lateral carinae of pronotum not or hardly visible in dorsal view, with punctures very dense, larger than puncture intervals. Minute point of scutellum exposed. Elytra nearly entirely covering abdomen, weakly narrowed apically, with lateral margins evenly, weakly rounded; adsutural area flat and narrow; sutural stria punctate, entire, bent at base and extended to form very shallow basal stria reaching about elytral mid-width, widely separated from lateral stria; lateral stria densely punctate. Elytral disc not microsculptured; punctation all over dense and fairly coarse, punctures not or only somewhat larger than those on pronotum,

well delimited, puncture intervals larger than puncture diameters. Hind wings fully developed. Hypomeron not microsculptured, distinctly punctate except on smooth area along upper margin, with punctures about as large pronotal punctures, most puncture intervals larger than puncture diameters. Mesoventrite punctate, without median ridge, fused with metaventral process. Mesanepisternum punctate, punctures distinct, as large as on pronotum and hypomeron. Mesepimeron with dense row of puncture along anterior margin, about three times as long as wide and four times as long as interval to coxa. Middle of metaventrite convex and finely punctate; punctures on lateral part of metaventrite conspicuous, as on mesanepisternite and hypomeron. Submesocoxal lines parallel, with marginal punctures not smaller than punctures on lateral area of metaventrite and not extended laterally along margin of metaventrite. Submesocoxal areas about 0.03 mm long, as fourth of shortest distance to metacoxae. Metanepisternum flat, fused with metaventrite, its margin indicated by outer puncture row of metaventrite. Tibiae straight. Abdomen not microsculptured. Ventrite I with punctation as that on lateral area of metaventrite, basal punctures not enlarged, elongate, basal striae or wrinkles absent. Following ventrites finely punctate.

Male characters: Protarsomeres I to III slightly widened. Aedeagus (Figs 17-19) 0.43 mm long, symmetrical, with ventral side of apical process sinuate and bent at tip (lateral view). Parameres nearly straight and slightly narrowed apically in dorsal view (Fig. 18), evenly broad and weakly sinuate in lateral view. Internal sac with complex sclerites, lacking membranous scale- or denticle-like structures.

Habitat: South slope of G. Dab, secondary forest on limestone, soil and very humid leaf litter.

Distribution: Indonesia: Moluccas, Tanimbar Islands.

Remarks: The aedeagal characters suggest relationship with *B. incurva*. Unfortunately, the sole available male has the internal sac extruded. Therefore, its structure cannot be compared to that of internal sacs in resting position. This species may be easily distinguished from *B. incurva* by the elytra having entire sutural striae curved at bases and extended laterally to form basal striae. The mesepimeron punctate along anterior margin is a feature shared only with *B. punctigera*.

Key to the Moluccan species of *Baeocera*

1 Metanepisterna distinct, separated clearly from metaventrite by a suture. Lateral parts of metaventrite very finely punctate 2
- Metanepisterna indistinct, fused with metaventrite. Lateral parts of metaventrite coarsely punctate 4
2 Body about 1.6-1.7 mm long. Ventrite I with basal wrinkles ..... *B. agostii* Löbl
- Body 1.05-1.40 mm long. Ventrite I lacking basal wrinkles 3
3 Body 1.05 mm long. Basal striae of elytra broadly separated from lateral striae ..... *Baeocera* sp. A
- Body about 1.40 mm long. Basal striae of elytra joined with lateral striae ..... *Baeocera* sp. B
4 Pronotum and hypomera conspicuous punctate, with punctures well visible at magnification 20 times 5
- Pronotum and hypomera with inconspicuous punctation hardly visible at magnification 40 times, or impunctate 7
5 Elytra with sutural striae shortened, starting well posterior of level of point of scutellum, basal striae absent 6
- Elytra with sutural striae entire and extended along basal margins to form basal striae ... *B. punctiventris* sp. nov.
6 Mesepimera impunctate. Body length about 1.3-1.4 mm ..... *B. notata* sp. nov.
- Mesepimera punctate. Body length about 1.2 mm ..... *B. punctigera* sp. nov.
7 Elytra with sutural striae shortened, starting well posterior of level of scutellar tip 9
- Elytra with sutural striae entire, starting at elytral bases 11
9 Body length 0.90 mm. Apical fourth of parameres widened (dorsal view) ..... *B. kaibesara* Löbl
- Body length about 1.20-1.35 mm. Apical fourth of parameres not widened 10
10 Tip of median lobe bent, tip of parameres not bent dorsally ..... *B. vicina* Löbl
- Tip of median lobe not bent, tip of parameres bent dorsally ..... *B. incurva* sp. nov.
11 Elytra with basal striae entire, joined to lateral striae ..... *B. paucivestis* sp. nov.
- Elytra with basal striae broadly separated from lateral striae 12
12 Aedeagus with tip of median lobe not bent ventrally 13
- Aedeagus with tip of median lobe bent ventrally 14
13 Body about 1.20-1.35 mm long. Apices of parameres widened (lateral view) ..... *B. vafra* Löbl
- Body about 1.0-1.10 mm long. Apices of parameres not widened (lateral view) ..... *B. variata* Löbl
14 Antennomere XI about 1.3 times as long as antennomere X. Aedeagus with flagellar guide-sclerite not widened apically ..... *B. yamdena* Löbl
- Antennomere XI about 1.1 times as long as antennomere X. Aedeagus with flagellar guide-sclerite widened apically ..... *B. humicola* sp. nov.

Baeocera sp. B

Material examined: MHNG; 1 female; MALUC: Kai Besar Island, G. Dab, leaf litter, 400 m, 5.IX.1981, D. Agosti, F911046.

Remarks: This is the second Moluccan species of *Baeocera* remaining unnamed, in absence of at least one male specimen (see "*Baeocera* sp. A" in Löbl, 2015a). It is similar to the Papuan *B. curta* Löbl, 2002, differs by the less arcuate suture of the metanepisterna and the ventrite I lacking basal striae. Thus, it may be an undescribed species. *Baeocera curta* has a complex aedeagus providing reliable specific characters which are quite unlike those of members of the *Baeocera lenta* group and of *B. agostii*. The specimen has slightly prominent apical inner apical angles of the elytra, a character noted for the first time in *Baeocera*. It may be sexual, as it is in some species of *Scaphisoma* Leach.

Scaphisoma Leach, 1815

Remarks: This species-rich genus is nearly world-widely distributed. At present, 18 species are known from the Moluccas (Löbl, 2015a), all but *S. luteomaculatum* Pic, 1915 and *S. coarctatum* Löbl, 2003 possibly endemic. The studied material comprises two additional species, one known previously from Queensland, and a new one.

Scaphisoma sublimbatum Löbl, 1977

Scaphisoma sublimbatum Löbl, 1977: 57.

Material examined: MHNG; 2 males; MALUK: Aru Isl., Wokam, 5 km E. Mt. Sungai, 22.VIII.1981, D. Agosti, F91936.

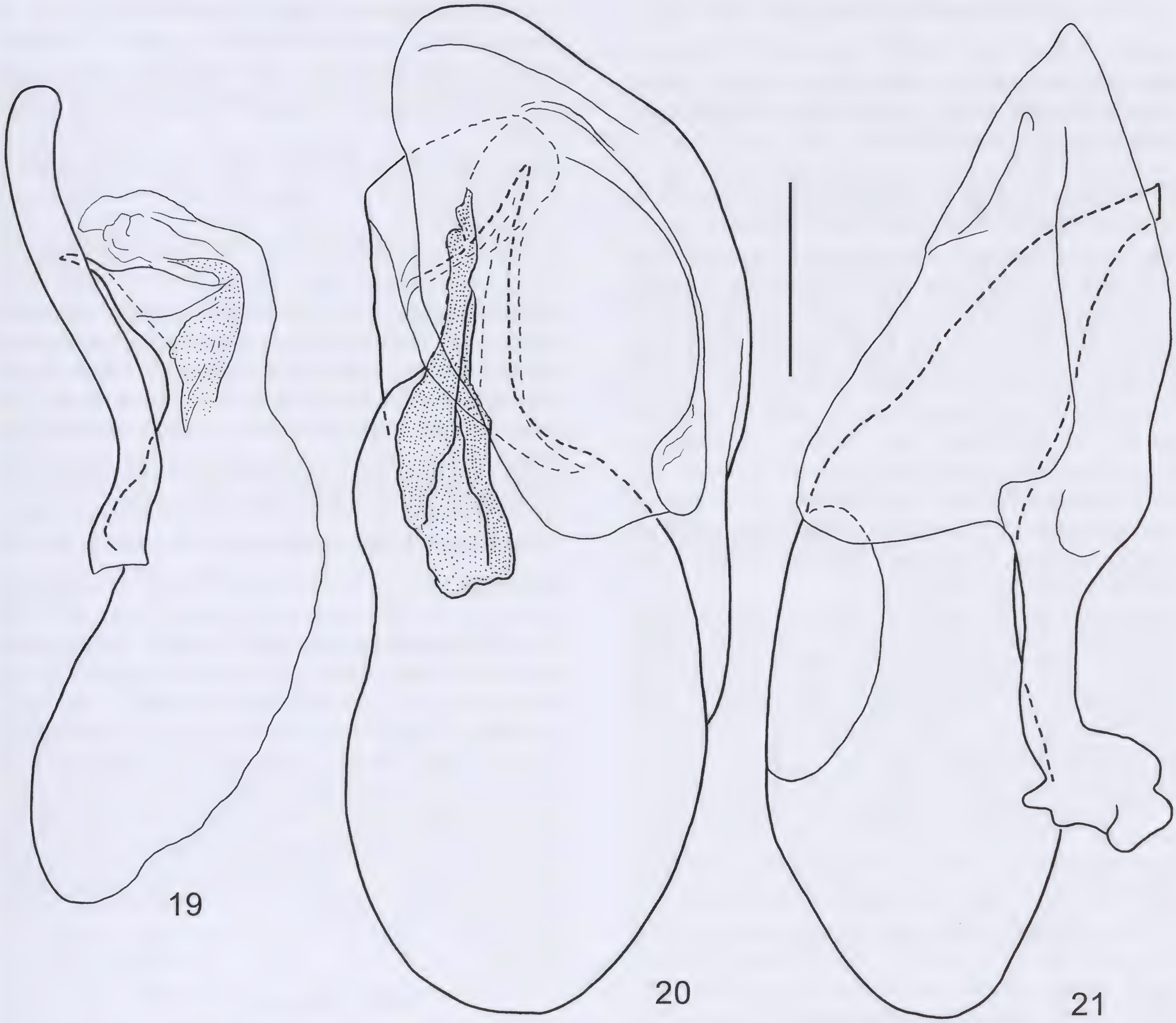
Redescription: Length 1.53-1.75 mm, width 1.02-1.22 mm. Head, thorax and most abdomen dark brown, apex of abdomen yellowish. Elytra on adsutural area, along basal and lateral margins, and on transverse stripe in middle as dark as pronotum, in apical sixth to fifth light brown, each with two large, irregular, transverse yellowish spots. Anterior spots extending to middle third of elytral length, posterior spot starting about at level of apical third of elytral length. Femora light brown, tibiae, tarsi and antennae yellowish. Length/width ratios of antennomeres as: III 12/10: IV 27/8: V 50/9: VI 50/9: VII 57/16: VIII 38/10: IX 53/14: X 53/15: XI 60/14. Pronotum not microsculptured, with lateral margins strongly, evenly rounded, lateral margin carinae throughout visible in dorsal view, lateral margin carinae impunctate, discal punctation fine, sparse, most puncture intervals about 2 to 4 times as large as puncture diameters, punctures shallow, not well delimited, visible at 30 times magnification. Exposed point of scutellum minute. Elytra not microsculptured, with lateral margins evenly rounded, lateral margin carinae exposed in dorsal view, lateral margin striae impunctate, apical margins truncate, inner apical angles not prominent, situated in level with outer apical angles, marginal crenulation very fine, distinct, sutural striae deep, bent at bases and extending laterally to form basal striae reaching outer half of basal width, widely separated from lateral striae, sutural striae parallel, impunctate, adsutural areas flat, each with single, very fine and sparse puncture row, discal punctures irregular, fairly fine and dense, coarser than pronotal or adsutural punctures, not forming rows, puncture intervals mostly distinctly larger than puncture diameters. Hind wings fully developed. Hypomera not microsculptured, impunctate. Mesepimon about 4 times as long as wide and somewhat shorter than interval to mesocoxa. Metaventrite not microsculptured. Median part of metaventrite convex between mesocoxae, flattened apically, with three fovea-like apical impressions, middle impression larger and situated slightly anterior lateral impressions, often joint to short mesal stria; punctation indistinct, sparse and extremely fine on centre and on lateral areas of metaventrite. Lateral parts of metaventrite lacking antecoxal puncture rows. Submesocoxal area 0.02 mm long, about as sixth of shortest interval to metacoxa. Submesocoxal line parallel, densely and coarsely punctate, punctures extended laterally along anterior margin of metaventrite. Metanepisterna slightly convex, impressed along nearly straight suture, narrowed anteriad. Tibiae straight. Abdomen not microsculptured, with hardly visible punctation (at 100 times magnification). Ventrite I with submetacoxal area extremely narrow, about 0.01-0.02 mm long, narrowed mesally and as fifteens of interval to apical margin of ventrite; marginal punctures coarse.

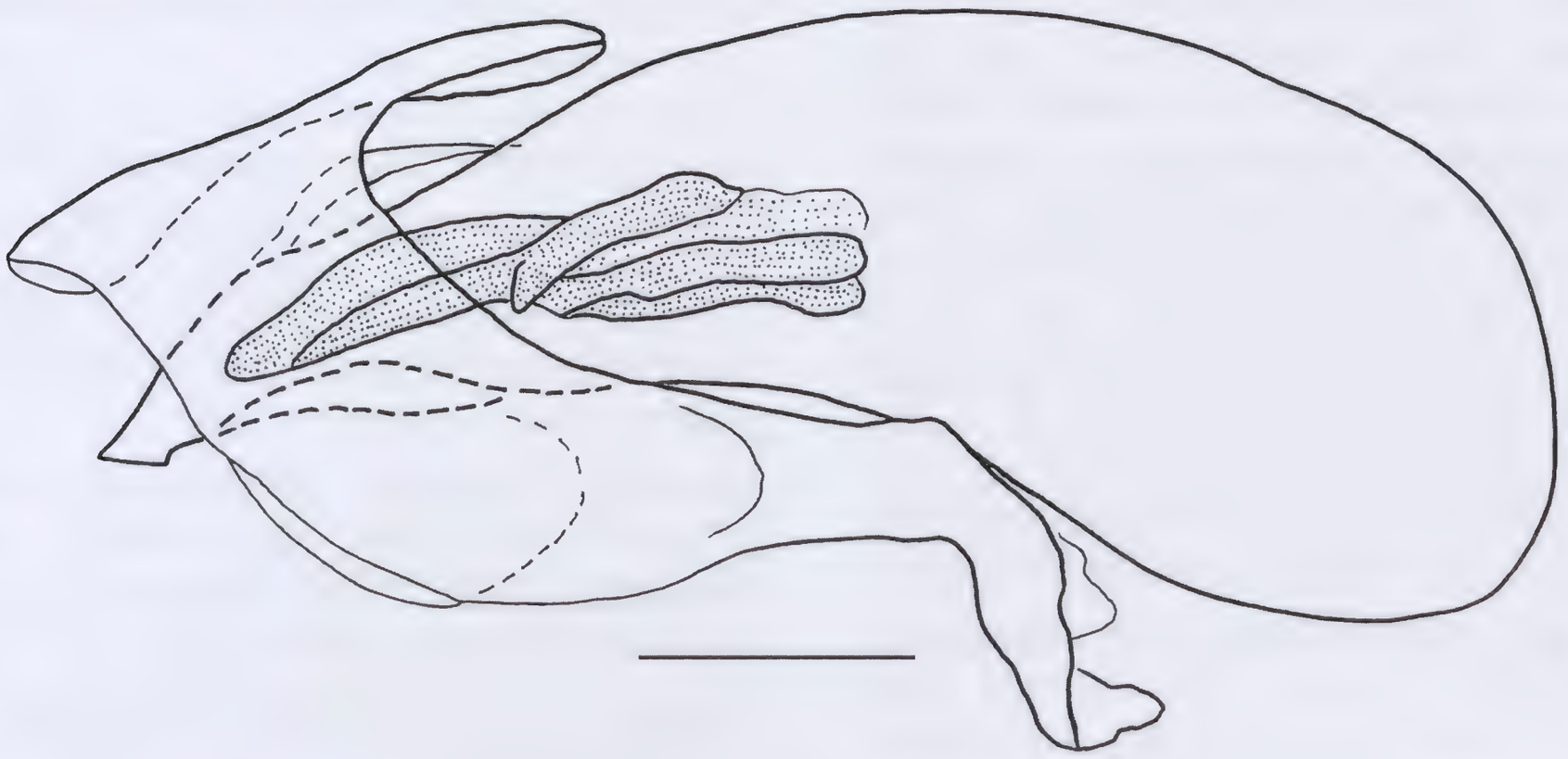
Male characters: Protarsomeres I to III and meso-tarsomeres I and II strongly widened, basal tarsomeres nearly as wide as apices of tibiae. Apical margin of ventrite VI trilobed, mesal lobe triangular, about 0.10 mm long, lateral lobes shorter and rounded.

Habitat: Secondary/primary forest on limestone, leaf litter on rather dry soil, understory *Pandanus*.

Distribution: Australia: Queensland; Indonesia: Moluccas, Aru Islands.

Remarks: This species is a member of the *S. unifasciatum* group defined in Löbl, 1977. In addition to *S. sublimbatum*, the group includes four New Guinean species: *S. audax* Löbl, 1975, *S. quadripunctatum* (Pic, 1956), *S. unifasciatum* Pic, 1956, and *S. unimaculatum* Löbl, 1975. An additional species is described below. The original description of the external features *S. sublimbatum* was brief and limited to comparation to the similar *S. audax*. Therefore, it is supplement.





Figs 19-22. *Baeocera punctiventris* sp. nov. (19) Aedeagus in lateral view. Figs 20-22. *Scaphisoma donati* sp. nov. (20, 21) Aedeagus in dorsal and lateral views, scale bars 0.2 mm. (22) Median lobe with left paramere, without internal sac.

Scaphisoma donati sp. nov.

Figs 20-23

Material examined: *Holotype*; MHNG; male; MALUC: Tanimbar Isl., Sangliat Krawai E Yamdena, 19.IX.81 D. Agosti F911120.

Etymology: The species is named in honour of its collector, Donat Agosti (Bern, Switzerland).

Diagnosis: The species is defined by the following characters in combination: Body-length nearly 2 mm, body dark reddish-brown, not microsculptured; elytra with sutural striae parallel, basal striae entire, joined to lateral striae; mesepimeron shorter than interval between its tip and mesocoxa; metaventrite distinctly punctate on transverse area anterior of metacoxal process, lacking fovea-like impressions; submesocoxal and submetacoxal areas very narrow, with parallel lines; aedeagus as Figs 20-23, strongly asymmetrical, parameres lobed, overlapping apex of median lobe, internal sac strongly sclerotized.

Description: Length 1.94 mm, width 1.33 mm. Head and most of body nearly evenly dark reddish-brown. Apex of abdomen and appendages lighter. Antennomere II about four times as long as antennomere III. Length/ width ratios of antennomeres as: III 9/10: IV 38/8: V 56/9: VI 52/8: VII 56/13: VIII 44/8: IX 57/15: X 52/14: XI 58/15. Pronotum and elytra not microsculptured. Pronotum with lateral margins rounded, lateral margin carinae not visible in dorsal view, discal punctation dense and very fine, consisting of poorly delimited punctures. Minute point of scutellum exposed. Elytra moderately narrowed apically, lateral margin rounded, lateral margin carina clearly exposed in dorsal view only in basal third, inner apical angle about in level with outer apical angle, sutural margin not raised, adsutural area flat, not narrowed apically, with very fine puncture row; sutural striae curved at base and extended laterally to form basal striae joined to lateral striae, discal punctation irregular, fine, punctures not well delimited, puncture intervals mostly about twice to five times as large as puncture diameters. Hind winds reduced. Exposed tergites very finely punctate, not microsculptured. Hypomeron smooth. Mesepimeron about four times as long as wide, distinctly shorter than interval between its tip and mesocoxa. Metaventrite short, not microsculptured, slightly convex in middle. Mesocoxal process concealed with mesoventrite. Centre of metaventrite impunctate, fairly coarse punctures present on transverse area anterior metacoxal process, fovea-like impressions absent. Lateral parts of metaventrite very finely and sparsely punctate, punctures on lateral areas hardly visible, antecoxal puncture rows absent. Submesocoxal lines parallel, fairly coarsely punctured; submesocoxal area about 0.02 mm long, as tenth of shortest distance to metacoxa. Metanepiternum narrowed anteriad. Ventrite I with punctation very fine, similar to lateral parts of metaventrite; submetaxocal lines parallel, margined with coarse punctures; submetacoxal areas hardly 0.02 mm, about as tenth of shortest distance to apical margin.

Male characters: Ventrite VI with mesal process triangular, about 0.15 mm long. Protarsomeres and mesotarsomeres I to III distinctly widened, with tenant setae, protarsomeres I narrower than apices of protibiae. Aedeagus (Figs 20-23) 1.25 mm long, strongly sclerotized and strongly asymmetrical. Apical process of median lobe slightly inflexed, obliquely truncate at apex. Left paramere extended posterior of right paramere and overlapping most of apical process. Internal sac with robust, strongly sclerotized and irregularly narrowed rod.

Habitat: Kanary evergreen primary forest on limestone, 50 m, thick leaf litter with heavy mycorrhiza.

Distribution: Indonesia: Moluccas, Yamdena Island.

Remarks: This is a member of the *S. sublimbatum* group. It may be easily distinguished from the other five members of the group by the elytra lacking spots, the metaventrite lacking mesal stria and fovea-like impressions, the antennomeres XI about as large as the antennomeres IX, and the basal striae of the elytra entire, joined to the lateral striae, in combination. The aedeagal characters suggest close relationships to *S. quadripunctatum* (Pic, 1956), the shape of the truncate tip of the apical process of the median lobe is unique in the new species. Its reduced hind wings suggest narrow endemism.

Scaphobaeocera Csiki, 1909

Remarks: Members of this widely distributed genus are recorded for the first time from the Moluccas.

Scaphobaeocera schouteni Löbl, 1980

Scaphobaeocera schouteni Löbl, 1980: 223.

Material examined: MHNG; 1 male; MOLUK: Tanimbar, Kai Besar, G. Dab, 400 m, 5.IX.1981, D. Agosti.

Remarks: The species was based on a single specimen collected at Limbin, New Ireland, and remained unrecorded since. The shape of its flagellum is diagnostic (see Löbl, 1980: fig. 3).

Habitat: Secondary forests on limestone, very humid soil and leaf litter.

Distribution: Papua New Guinea: New Ireland; Indonesia: Moluccas, Kai Besar Island.

Scaphobaeocera plana sp. nov.

Figs 24-27

Material examined: *Holotype*; MHNG; male; MALUK: Kai Besar, G. Tukrau nr Bombay, 4.IX.81, D. Agosti F911035.
Paratype; MHNG; male; with the same data as the holotype but 5.IX. and F911046.

Etymology: The species epithet is a Latin adjective meaning flat.

Diagnosis: Body-length 0.90 mm long, body light brown, not microsculptured and not iridescent; antennomere VIII exceeding half-length of antennomere VII, antennomere XI slightly longer than antennomere X and nearly 3 times as long as wide; elytra lacking parasutural stria; hypomeron lacking longitudinal striae; aedeagus as Figs 24-27, with broad basal bulb, short, strongly sclerotized and bent apical process and short, bilobed apicodorsal plate, parameres expanded, notched mesally, internal sac with short, robust, incurved sclerite.

Description: Length 0.90 mm, width 0.52 mm, dorsoventral diameter 0.47 mm. Head, body, femora and tibiae nearly uniformly light brown, elytra somewhat lighter near apices, tarsi and antennae lighter than tibiae. Length/width ratios of antennomeres as: III 10/5: IV 13/5: V 14/5: VI 12/5: VII 23/10: VIII 13/8: IX 24/10: X 27/11: XI 33/12. Pronotum finely punctate, not microsculptured. Scutellum concealed. Elytra not iridescent, not microsculptured, lacking parasutural striae, sutural striae deep, curved near base, discal punctation coarser than pronotal punctation. Hypomera not microsculptured, smooth, lacking longitudinal stria. Mesoventrite with low mesal ridge. Metaventrite weakly convex between mesocoxae, lacking median stria; entire median area rather coarsely and densely punctate, with some punctures about as large as puncture intervals, pubescence short. Lateral parts of metaventrite very finely punctate, not microsculptured. Submesocoxal areas about 0.03 mm, as half of shortest interval to metacoxae, submesocoxal lines appearing impunctate. Metanepisterna about 0.05 mm wide, flat, not narrowed anteriad, impunctate, with straight suture reaching metepimera. Tibiae straight. Abdomen not microsculptured, very finely punctate, coarse basal punctures of ventrite I excepted.
Male characters: Protarsomeres I to III strongly widened, about as wide as apices of protibiae. Aedeagus as in Figs 24-27, 0.36-0.38 mm long. Apical process of median lobe short, curved and strongly inflexed, in apical section nearly perpendicular to basal bulb. Articular process not prominent. Dorsal side of basal bulb produced to form bilobed, strongly sclerotized plate. Internal sac with strongly sclerotized, proximally hook-like piece.

Habitat: Secondary forests on limestone, 200-400 m, dead log and leaf litter infested by fungi.

Distribution: Indonesia: Moluccas, Kai Besar Island.

Remarks: The species differs from most congeners by its body comparatively weakly convex, lacking microsculpture, and the elytra lacking parasutural striae, in combination. The aedeagal characters of *S. plana* are unique. The presence of a narrow apicodorsal process of the median lobe, the shape of the parameres and that of the sclerite of the internal sac lacking a flagellum are diagnostic. The generic assigned is therefore tentative. Several character states used to define the Scaphisomatini genera (see Leschen & Löbl, 2005) have not been verified as they may be seen only on slides of the head and thorax, requiring more available specimens.

Scaphobaeocera sp. 1

Material examined: MHNG; 1 male; MALUK: Aru Isl., Wokam, 5 km E Mt. Sungai, 22.8.1981, D. Agosti.

Remarks: This specimen possesses aedeagal characters similar to those of *S. notata* Löbl, 2017, from Papua New Guinea, and *S. lombokensis* Löbl, 2015. It differs from *S. notata* quite conspicuously by the uniformly light brown elytra, and from *S. lombokensis* by the parameres nearly evenly broad in lateral view and the ventrally bent tip of the median lobe. More material is needed to assess the variability of these characters.

Habitat: Secondary/primary forest on limestone, sea level, rather dry leaf litter; understory *Pandanus* palms.

Distribution: Indonesia: Moluccas, Aru Island.

Scaphobaeocera sp. 2

Material examined: MHNG; 1 female; MALUK: Tanimbar Isl., Yamdena, 22 km N Samlaki via Aram, Desa Lorulun, 11.IX.1981, D. Agosti.

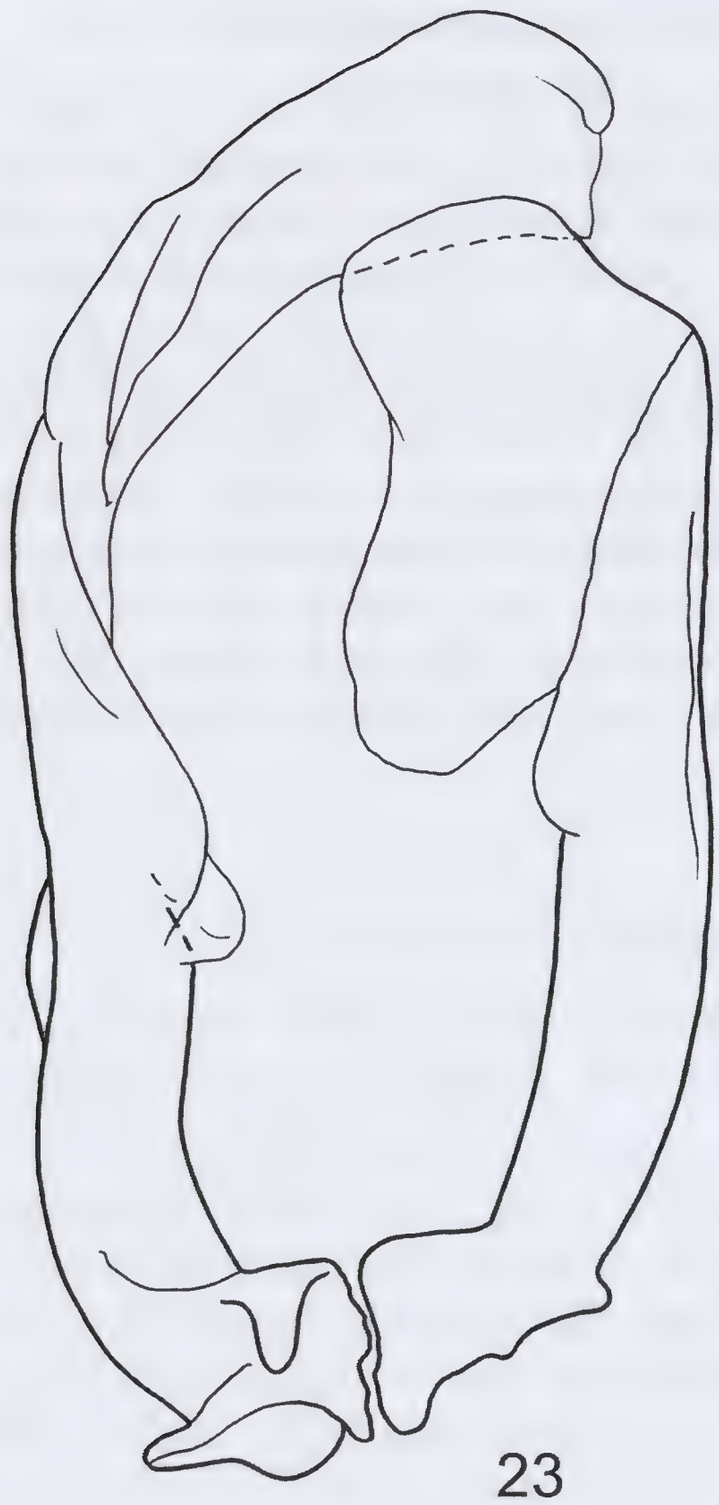
Remarks: This specimen would fall in the key to the New Guinean *Scaphobaeocera* (Löbl, 2017) under the couplet 5, to *S. antennalis* Löbl, 1975 and *S. remota* Löbl, 1981, and it shares with *S. remota* the elytra darkened apically and the antennomeres XI more than twice as long as the antennomeres X.

Habitat: Melaleuca open forest on limestone, leaf litter heavily infested by mycorrhiza.

Distribution: Indonesia: Moluccas, Tanimbar Island.

Scaphoxium Löbl, 1979

Remarks: Members of this widely distributed genus are here recorded for the first time from the Moluccas.



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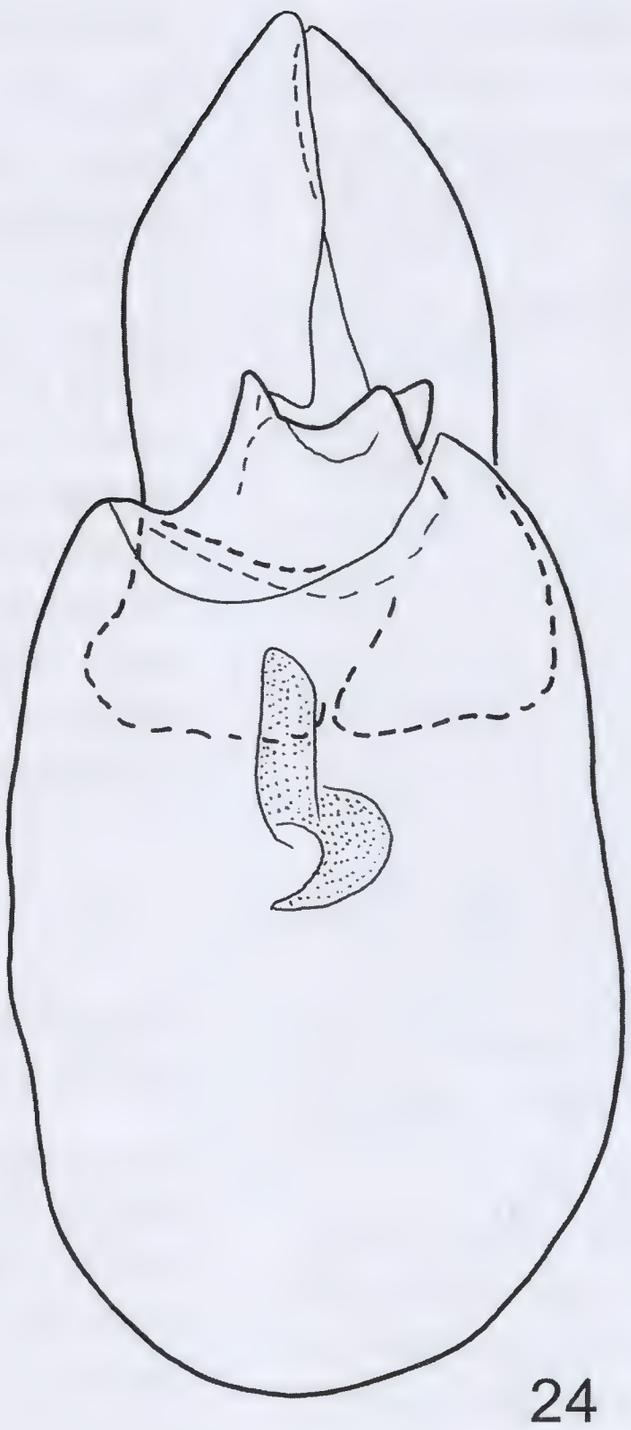

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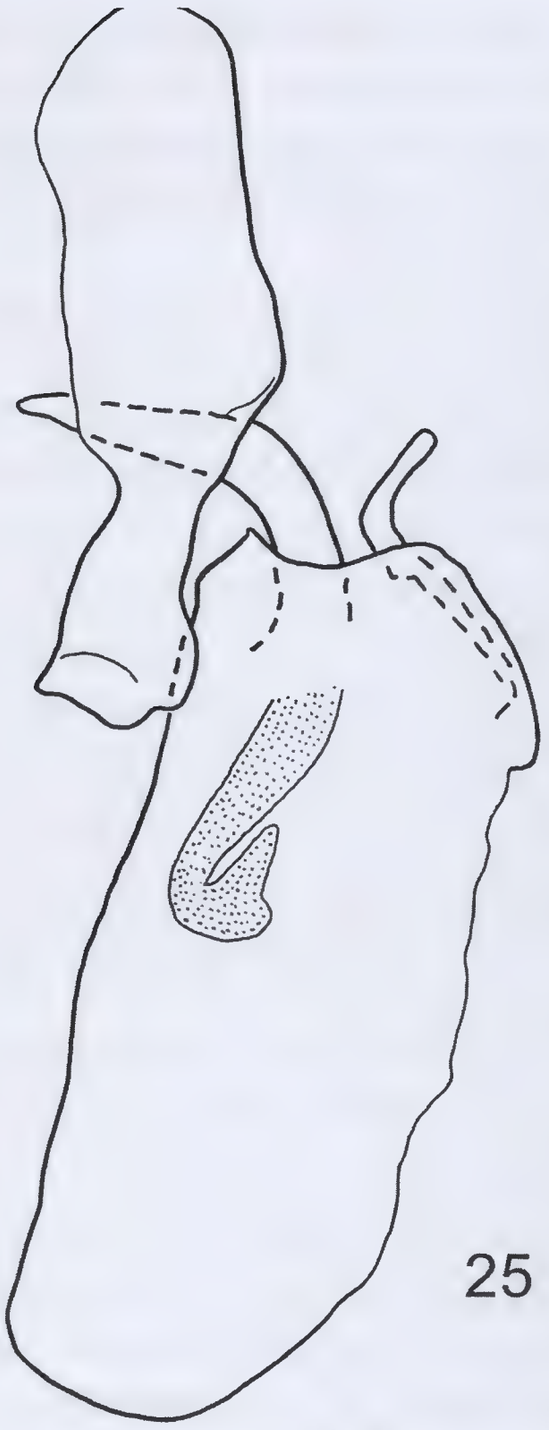

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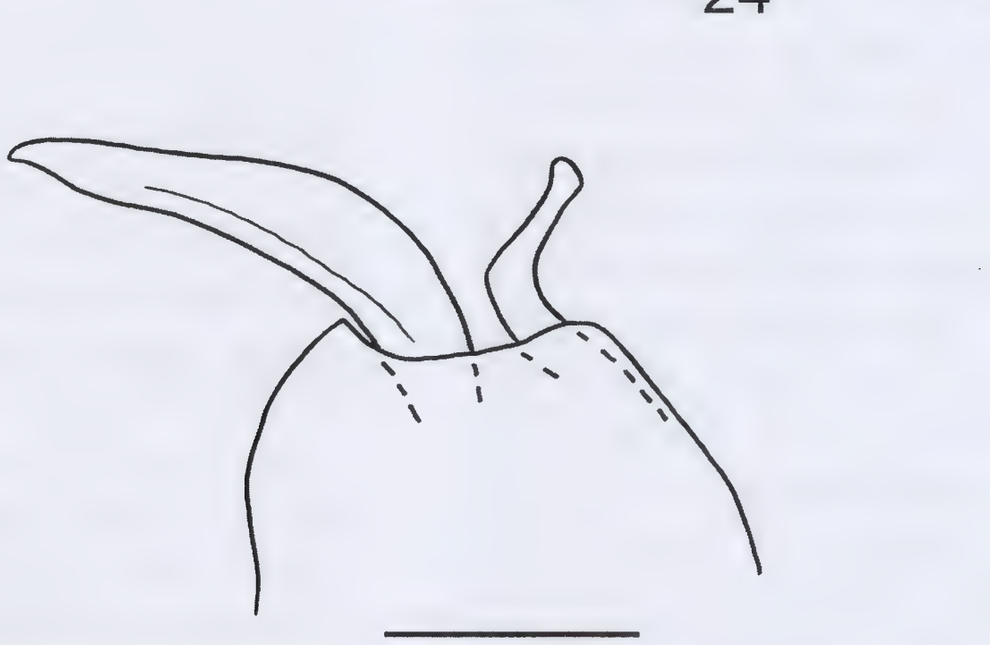

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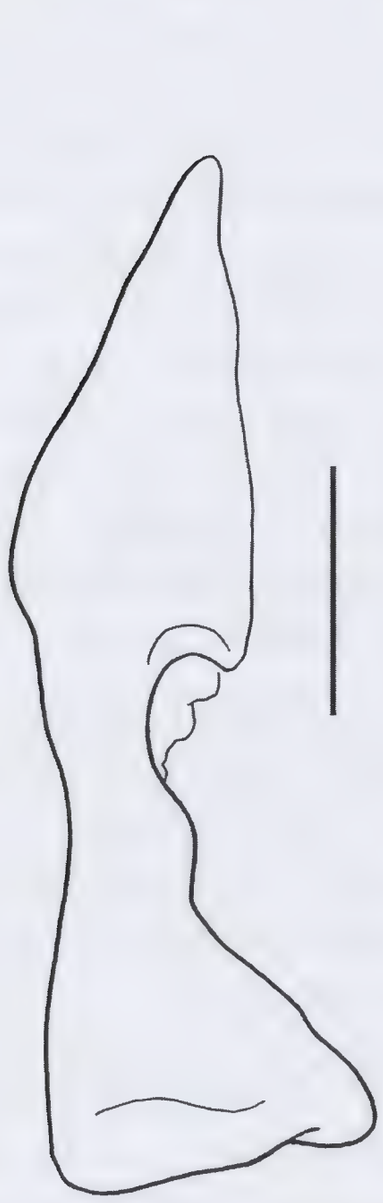

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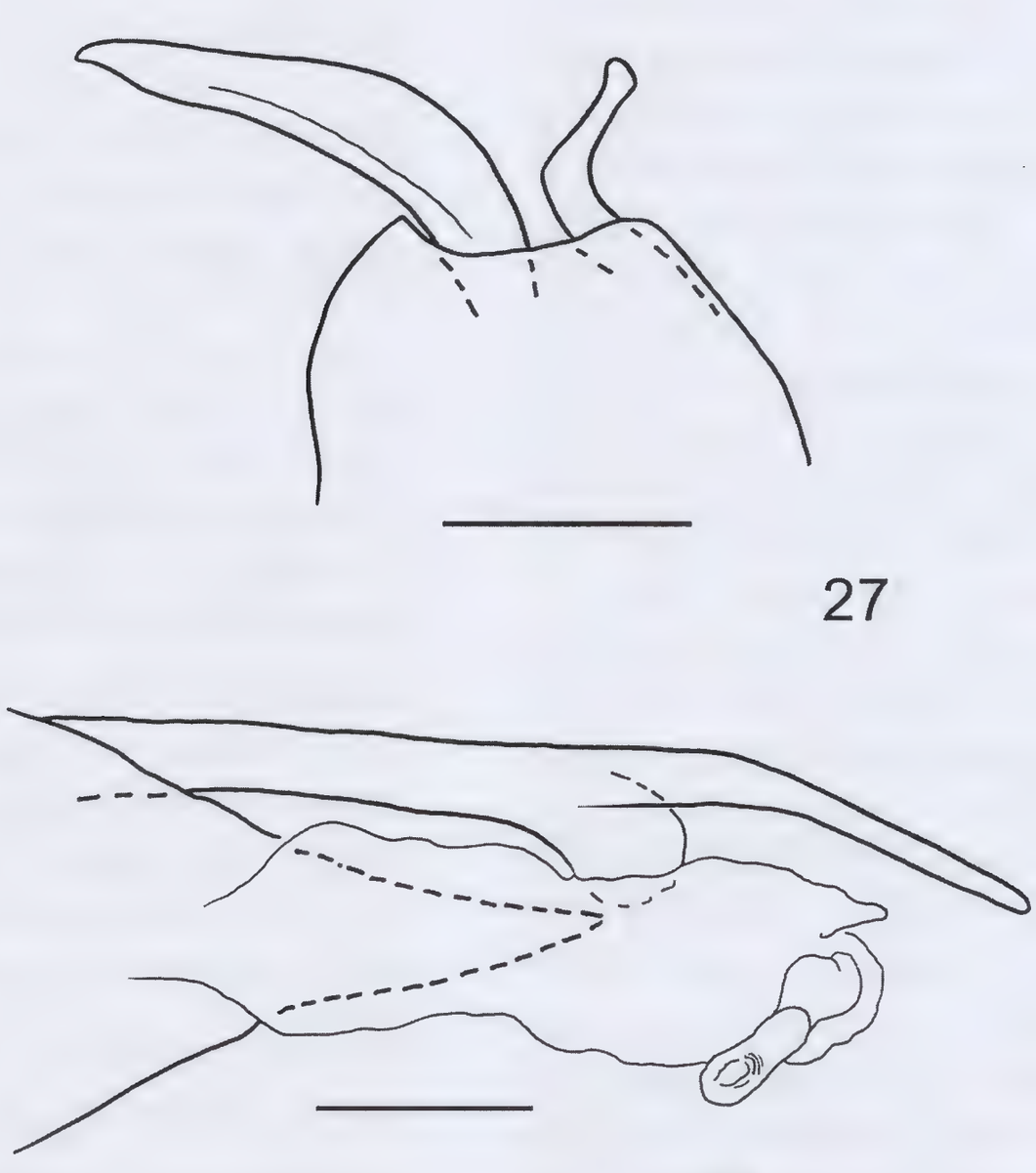

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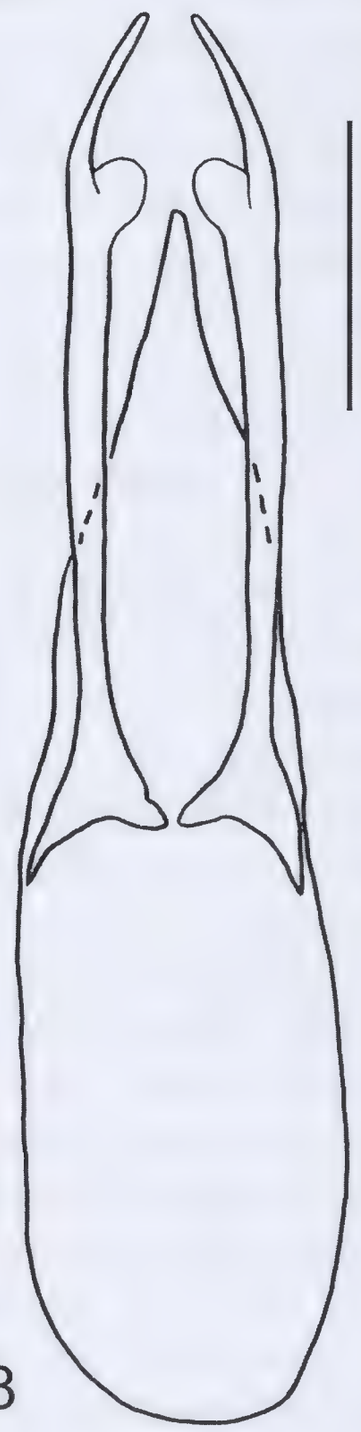

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Figs 23-29. *Scaphisoma donati* sp. nov. (23) Parameres in ventral view, scale bar = 0.2 mm. Figs 24-27. *Scaphobaeocera plana* sp. nov. (24, 25) Aedeagus in dorsal and lateral views, scale = 0.1 mm. (26) Paramere in ventral view, scale = 0.05 mm. (27) Apical part of median lobe, in lateral view, scale = 0.05 mm. Figs 28, 29. *Scaphoxium lobatum* sp. nov. (28) Aedeagus in ventral view, scale = 0.1 mm. (29) Apex of median lobe with extruded internal sac and right paramere, in dorsal view, scale = 0.05 mm.

Scaphoxium lobatum sp. nov.

Figs 28, 29

Material examined: *Holotype*; MHNG; male; MALUK: Aru Isl., Wokam, 5 km E Mt. Sungai, 22.8.1981, D. Agosti F91936.

Etymology: The species epithet is a Latin adjective meaning lobed.

Diagnosis: Body-length 1.35 mm; elytral punctation well delimited; hypomeron with longitudinal ridge; mesoventrite and metaventrite grooved mesally; lateral parts of the metaventrite bearing coarse punctures; submesocoxal area as long as shortest interval to metacoxa; abdomen with punctulate microsculpture; aedeagus as Figs 28, 29, with parameres broadly lobed at level of tip on median love, slightly narrowed posterior of lobe, internal sac lacking distinct sclerites and without scale-like or spine-like structures.

Description: Length 1.35 mm, width 0.67 mm, dorsoventral diameter 0.73 mm. Body uniformly dark brown, appendages lighter. Length/width ratios of antennomeres as: III 15/6: IV 15/6: V 25/6: VI 23/7: VII 38/10: VIII 28/8: IX 35/11: X 35/12: XI 43/13. Pronotal punctation dense and fine, distinct at 50 times magnification. Tip of scutellum exposed. Sutural striae starting posterior of basal fourth of elytra, evanescent in anterior 0.20 mm of elytral length. Elytral punctation and pubescence dense, visible at 25 times magnification, consist of sharply delimited punctures. Hypomeron very finely punctate on somewhat convex upper part, impunctate on flattened lower part; lower and upper parts separated by ridge extended anteriorly to level of procoxal mid-length. Mesoventrite grooved mesally. Mesanepisternum very finely punctate. Metaventrite grooved mesally, in middle very finely punctate. Lateral parts of metaventrite with punctation coarse and dense near submesocoxal lines, with punctures to parts larger than puncture intervals; punctation becoming sparser and fines laterad, areas along metanepisterna impunctate. Submesocoxal lines strongly arcuate, finely punctate. Submesocoxal areas 0.05 mm, about as long as shortest intervals to metacoxae. Metanepisterna not fused, with straight, finely punctate suture nearly touching margin of metepimera. Visible abdominal segments with distinct punctulate microsculpture. Exposed ventrites with very fine punctation, coarse row of basal punctures of ventrite I excepted.

Male characters: Protarsomeres I to III hardly widened. Aedeagus (Figs 28, 29) 0.51 mm long. Parameres each with large, rounded lobe at level of tip of median lobe, narrow and weakly bent posterior lobe, internal sac with plate-like structure, lacking spines or scales.

Habitat: Secondary/primary forest on limestone, rather dry leaf litter; understory *Pandanus* palms.

Distribution: Indonesia: Moluccas, Aru Islands.

Remarks: This species resembles *S. bilobum* Löbl, 2015 from Lombok which shares the shape of the parameres and the coarse punctation on lateral parts of the metaventrite. These two species differ in elytral punctation which is notably denser and consist of sharply delimited punctures in *S. lobatum.* The more relevant feature of *S. lobatum* is the internal sac lacking two pairs of strongly sclerotized pieces. The antennomeres III and IV appear slightly shorter in *S. lobatum*, a character not to be used as diagnostic until more material available to assess its variability more reliably. The length of the antennomere VI of *S. bilobum* was given in the original description as equal to that of the antennomere VII by error (Löbl, 2015b: 117), it is equal to that of the antennomere V.

Scaphoxium sp.

Materiel examined: MHNG; 1 female; MOLUK: Kai Besar, Bombay, G. Dab, 3.IX.1981, D. Agosti, F911019. – MHNG; 1 female; MOLUK: Kai Besar, G. Tukram, 300-500 m, 7.IX.1981, D. Agosti F911075.

Remarks: These two specimens differ notably from *S. lobatum* by the very finely punctate lateral parts of the metaventrite.

Habitat: Secondary forests on limestone; leaf litter and moss on fallen tree.

Distribution: Indonesia: Moluccas, Kai Besar Island.

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My cordial thanks are due to Donat Agosti (Bern, Switzerland), for his effort in collecting leaf litter beetles and donating the sampled specimens to the Geneva Muséum d'histoire naturelle. Christina Lehmann-Graber (Geneva, Switzerland) kindly assisted with the illustrations.

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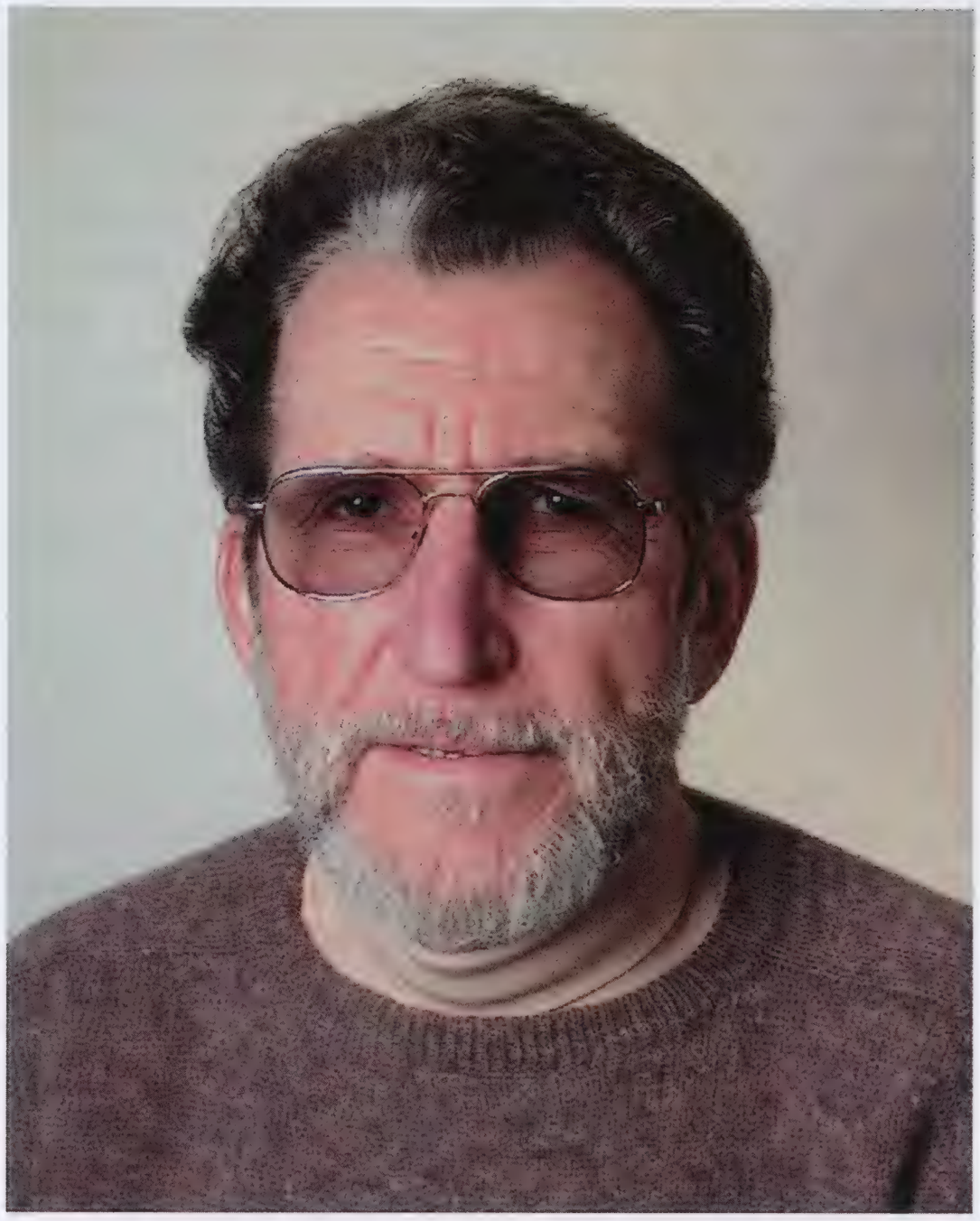
Antoine Senglet (10.IX.1927 - 29.III.2015), a little-known Swiss entomologist and arachnologist

It is unusual to write an obituary seven years after the death of a person, but we had only insufficient biographical data about Antoine Senglet until recently. Since we have received several requests for information about him during the last few years (mostly in connection with studies on spiders from Iran), and considering his long-lasting association with the Natural History Museum of Geneva (MHNG) and his remarkable contribution to its arthropod collections, we feel that there is a need to publish a short notice about his life and his scientific achievements.

Antoine Senglet was born on 19 September 1927 in the village of Le Muids (today Arzier-Le Muids), in the French-speaking Swiss canton of Vaud. He was very proud of his "Romand" identity. In his manuscripts submitted to the "Revue suisse de Zoologie" he usually mentioned "Romandie" in his postal address, which the subject editor had to replace with "Switzerland" in order to avoid any possible confusion with "Roumanie = Romania" and because the "Romandie" is not a country but a linguistically defined region. After undergoing primary education, young Antoine attended the "Ecole d'horticulture de Châtelaine" which then was moved to Jussy (also in the canton of Geneva) and became the "Haute école du paysage, d'ingénierie et d'architecture de Lullier". He subsequently went to work as a horticulturist in England and, when back in Geneva, took up various other jobs, including salesman for vacuum cleaners, pilot of small public boats (called "Mouettes genevoises") on Lake Geneva, and coalman. The latter he pursued until his retirement in 1993, when he moved to the village of Vich in the canton of Vaud to live in the house of his mother. He had a great interest in zoology, computers and all things technical, and since he received no formal academic education he became an autodidact. When one of us (PJS) first met A. Senglet in 1999, he arrived with a laptop holding a sophisticated self-programmed database (including detailed drawings and photographs of taxonomic characters) on the spider groups he was interested in.

Without the need to sustain a family (he had no wife or children, but a female companion later in his life),



Antoine Senglet in the early 1990s. Photo sent by A. Senglet to B. Huber in 1995.

A. Senglet usually worked in Geneva in autumn and winter, and then took several months off in spring and/or summer to visit warmer countries and pursue his passion: collecting arthropods. Between 1962 and 1970 he assembled a considerable collection of Odonata from Morocco, Spain, Portugal, France, Italy, Switzerland, ex-Yugoslavia, and Greece. Surprisingly he never published anything on this collection or on other Odonata. In 1978 he sold the collection to the MHNG. He quite abruptly abandoned his interests in Odonata in favour of another, even deeper passion which he pursued for the rest of his life: Araneae. In 1971 he started to publish on faunistics and taxonomy of spiders, later he also turned to mating behaviour and coupling mechanisms between male and female copulatory organs. Between 1967 and 2013 he

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collected thousands (if not tens of thousands) of spiders in the southern half of Europe (Spain, Portugal, France, Italy, Switzerland, ex-Yugoslavia, Romania, Bulgaria, Greece, Turkey), Morocco, Iran and Afghanistan. In many of these countries he could – and had to – communicate with the locals in their own language. Apart from being francophone, he was fluent in English and Greek, and he had basic knowledge of German, Russian and Persian. In 1973 he made an agreement with Claude Besuchet (1930-2020) and Villy Aellen (1926-2000), former curator of the Department of Entomology 2 and former director of the MHNG, respectively, which provided the financial basis for two extensive collecting trips to Iran in 1973 and 1974, and one to Iran and Afghanistan in 1975. The MHNG purchased the beetles (about half of them meanwhile mounted on cardboard), ants, cockroaches, earwigs, springtails, millipedes, centipedes, mites, pseudoscorpions, and other groups (of which little material is present) that A. Senglet brought back from these trips, and he kept the spiders to himself. It is unclear whether he also collected Opiliones from Iran, a group that is not included in his collection. Three times A. Senglet drove all the way from Geneva to Iran (in these days more open to westerners than at the moment) and back again in a Renault R4, into which he squeezed not only his long legs but also a bed and a refrigerator, and out of which he operated by collecting by hand, with a Winkler/Moczarski eclector and with a backpack aspirator (= suction apparatus). All specimens were preserved in alcohol. The "non-spiders" were sorted and labelled by MHNG staff; the spiders (which he retained) were neatly labelled and separated to families by himself. A considerable portion of the spiders he also identified to species or genus level. In general his material is well preserved, often species are represented by large series from numerous localities, and geographical coordinates are given, which usually allow to identify localities even if their names have changed. When his private collection was donated to the MHNG and arrived on 15 August 2014, it looked overwhelming in terms of volume and specimen numbers, but actually it was all nicely prepared for being incorporated into the spider collection of the museum, a process now complete. Senglet himself published on some of the pholcid spiders he collected in Iran and Afghanistan (besides pholcids, tetragnathids and gnaphosids from the Mediterranean Region). Through the mediation of the MHNG several other colleagues have studied or are currently examining other parts of this collection: Bernhard Huber further pholcids, Andrei Tanasevitch the linyphiids, Dmitri Logunov the salticids, philodromids and some lycosids, and Alireza Zamani & co-authors most of the remaining spiders. Selvin Dashdamirov has studied Senglet's pseudoscorpions from Afghanistan and is currently working on those from Iran; Adrian Smolis & Dariusz Skarzynski published on Senglet's neanurid springtails from Iran; several coleopterologists published on Senglet's beetles from

Antoine Senglet (left) and Andrei Tanasevitch (right; corresponding member of the MHNG) during a meeting in the spider collection of the MHNG on 21.XI.2008. Photo by P.J. Schwendinger.

Iran and Afghanistan. Thus, the collections of A. Senglet have proved to be a treasure trove for various taxonomic groups; much has already been published on it – more will hopefully follow in the coming years. His sampling of the previously little-known spider fauna of Iran is of special scientific importance. Alireza Zamani (Tehran, Iran), who is currently working on this fauna for a Ph. D. project at the University of Turku (Finland) and who has examined all Iranian spiders available in scientific collections, rates Senglet's collection, though mostly taken from the northern part of the country, as by far the most extensive and diverse in the world.

Antoine Senglet visited the MHNG whenever he needed to borrow specimens, deposit type specimens that he had described, pick up or bring back specimens which he borrowed from other museums and which were sent to the MHNG, discuss his manuscripts submitted to the "Revue suisse de Zoologie" with the editors, and when he had to take SEM-micrographs.

Back from a collecting trip to Greece in July 2013, A. Senglet suffered a stroke from which he never fully recovered and which left him confined to a wheelchair. He was admitted to a care facility in Yens (canton of Vaud), and when he arrived there he demanded to be allowed to bring along his spider collection. Quite understandably this was refused – it would have completely filled his

room. On 29 March 2015 he peacefully passed away listening to his beloved opera music. His body was cremated and his ashes scattered in the garden of his house. He will be remembered by his colleagues, friends and siblings (brother and sister) as a quiet and shy (though occasionally fairly outspoken), rational and dedicated person, and by the arachnological community as an exceptionally prolific collector and as an arachnologist who produced very detailed, high-quality illustrations and descriptions of taxonomic characters (non of his taxa names have so far been synonymized) and genital coupling mechanisms. His scientific legacy lasts on in the collections of the MHNG.

Acknowledgements

We are very grateful to Lilette Déglon (Morges, Vaud, Switzerland; A. Senglet's sister) and to Claire-Lise Bouquet Studer and Fernand Studer (Combe Varin, Neuchâtel, Switzerland; friends of A. Senglet since 1975) for providing biographical information. The latter two also took care of A. Senglet's spider collection after his stroke. Ivan Löbl (Veyrier, Geneva, Switzerland) kindly sent us a list of beetle species dedicated to A. Senglet and explained his association with the MHNG. Bernhard Huber (Zoologisches Forschungsmuseum Alexander König, Bonn, Germany) sent us a photo of A. Senglet and provided additional information. John Hollier (MHNG) checked the English text.

Peter J. Schwendinger & Christian Monnerat
Geneva, 23 November 2021

Appendix 1: Scientific publications by A. Senglet

Huber B.A., Senglet A. 1997. Copulation with contralateral insertion in entelegyne spiders (Araneae: Entelegynae: Tetragnathidae). *Netherlands Journal of Zoology* 47(1): 99-102. DOI: 10.1163/156854297X00274

Senglet A. 1971. Note sur les Pholcidae (Arachn.) de Grèce. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 44(3-4): 345-359. DOI: 10.5169/seals-401666

Senglet A. 1973a (for 1972). Note sur les *Pachygnatha* (Araneae: Tetragnathidae) de la péninsule ibérique. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 45(4): 301-305. DOI: 10.5169/seals-401693

Senglet A. 1973b (for 1972). Note sur les *Spermophora* (Araneae: Pholcidae) méditerranéens. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 45(4): 307-319. DOI: 10.5169/seals-401694

Senglet A. 1973c. Note sur *Spermophora elevata* Simon et description d'une nouvelle espèce: *Spermophora simoni* (Araneae: Pholcidae). *Bulletin du Muséum National d'Histoire Naturelle de Paris* (3) 125: 683-686.

Senglet A. 1974. *Pholcus* nouveaux d'Iran (Araneae: Pholcidae). *Revue suisse de Zoologie* 81: 803-812.

Senglet A. 2001. Copulatory mechanisms in *Hoplopholcus*, *Stygopholcus* (revalidated), *Pholcus*, *Spermophora* and *Spermophorides* (Araneae, Pholcidae), with additional faunistic and taxonomic data. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 74(1-2): 43-67. DOI: 10.5169/seals-402796

Senglet A. 2004. Copulatory mechanisms in *Zelotes*, *Drassyllus* and *Trachyzelotes* (Araneae, Gnaphosidae), with additional faunistic and taxonomic data on species from southwest Europe. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 77(1-2): 87-119. DOI: 10.5169/seals-402861

Senglet A. 2008. New species of *Pholcus* and *Spermophora* (Pholcidae, Araneae) from Iran and Afghanistan, with notes on mating mechanisms. *Revue suisse de Zoologie* 115(2): 355-376. DOI: 10.5962/bhl.part.80432

Senglet A. 2011. New species in the *Zelotes tenuis*-group and new or little-known species in other *Zelotes* groups (Gnaphosidae, Araneae). *Revue suisse de Zoologie* 118: 513-559. DOI:10.5962/bhl.part.117816

Senglet A. 2012. *Civizelotes* new genus, and other new or little-known Zelotinae (Araneae, Gnaphosidae). *Revue suisse de Zoologie* 119(4): 501-528. DOI: 10.5962/bhl.part.150203

Appendix 2: Spider taxa described by A. Senglet

N.B.: The secondary types for all these species, and the primary type for all species except for *Spermophorides simoni* (holotype probably in the Muséum National d'Histoire naturelle in Paris), are deposited in the spider collection of the MHNG.

Civizelotes Senglet, 2012 [Gnaphosidae]
Civizelotes ibericus Senglet, 2012 [Gnaphosidae]
Civizelotes medianoides Senglet, 2012 [Gnaphosidae]
Heser hispanus Senglet, 2012 [Gnaphosidae]
Hoplopholcus minotaurinus Senglet, 1971 [Pholcidae]
Hoplopholcus minous Senglet, 1971 [Pholcidae]
Pachygnatha bonneti Senglet, 1973 [Tetragnathidae]
Pachygnatha simoni Senglet, 1973 [Tetragnathidae]
Pachygnatha sundevalli Senglet, 1973 [Tetragnathidae]
Pachygnatha tullgreni Senglet, 1973 [Tetragnathidae]

Pholcus afghanus Senglet, 2008 [Pholcidae]
Pholcus armeniacus Senglet, 1974 [Pholcidae]
Pholcus arsacius Senglet, 2008 [Pholcidae]
Pholcus caspius Senglet, 2008 [Pholcidae]
Pholcus cophenius Senglet, 2008 [Pholcidae]
Pholcus creticus Senglet, 1971 [Pholcidae]
Pholcus djelalabad Senglet, 2008 [Pholcidae]
Pholcus elymaeus Senglet, 2008 [Pholcidae]
Pholcus hyrcanus Senglet, 1974 [Pholcidae]
Pholcus hystaspus Senglet, 2008 [Pholcidae]
Pholcus kandahar Senglet, 2008 [Pholcidae]
Pholcus medicus Senglet, 1974 [Pholcidae]
Pholcus parthicus Senglet, 2008 [Pholcidae]
Pholcus persicus Senglet, 1974 [Pholcidae]
Spermophora persica Senglet, 2008 [Pholcidae]
Spermophora senoculatoides Senglet, 2008 [Pholcidae]
Spermophorides huberti (Senglet, 1973) [Pholcidae]
Spermophorides mammata (Senglet, 1973) [Pholcidae]
Spermophorides mediterranea (Senglet, 1973) [Pholcidae]
Spermophorides petraea (Senglet, 1973) [Pholcidae]
Spermophorides simoni (Senglet, 1973) [Pholcidae]
Spermophorides valentiana (Senglet, 1973) [Pholcidae]
Stygopholcus photophilus Senglet, 1971 [Pholcidae]
Zelotes alpujarraensis Senglet, 2011 [Gnaphosidae]
Zelotes baeticus Senglet, 2011 [Gnaphosidae]
Zelotes chaniaensis Senglet, 2011 [Gnaphosidae]
Zelotes cordubensis Senglet, 2011 [Gnaphosidae]
Zelotes egregioides Senglet, 2011 [Gnaphosidae]
Zelotes hispaliensis Senglet, 2011 [Gnaphosidae]
Zelotes laconicus Senglet, 2011 [Gnaphosidae]
Zelotes pediculatoides Senglet, 2011 [Gnaphosidae]

Appendix 3: Arthropod taxa named after A. Senglet

Anemadus sengleti Giachino & Vailati, 1993 [Coleoptera, Leiodidae]
Bembidium sengleti Toledano & Marggi, 2007 [Coleoptera, Carabidae]
Brachygluta sengleti Besuchet, 1969 [Coleoptera, Staphylinidae]
Cataleptoneta sengleti (Brignoli, 1974) [Araneae, Leptonetidae]
Catops sengleti Giachino & Vailati, 2000 [Coleoptera, Leiodidae]
Crossopriza sengleti Huber, 2022 [Araneae, Pholcidae]
Deutonura sengleti Smolis, 2020 [Collembola, Neanuridae]
Epuraea sengleti Audisio, 1991 [Coleoptera, Nitidulidae]
Erigonoplus sengleti Tanasevitch, 2008 [Araneae, Linyphiidae]
Geostiba sengleti Pace, 1983 [Coleoptera, Staphylinidae]
Leptusa sengleti Pace, 1984 [Coleoptera, Staphylinidae]
Nargus sengleti Giachino & Vailati, 2000 [Coleoptera, Leiodidae]
Nazeris sengleti Bordoni, 1975 (a synonym of *Nazeris ibericus* C. Koch, 1940) [Coleoptera, Staphylinidae]
Otiorhynchus sengleti Smreczyński, 1977 [Coleoptera, Curculionidae]
Pelicinus sengleti Platnick, Dupérré, Ott, Baehr & Kranz-Baltensperger, 2012 [Araneae, Oonopidae]
Persilena sengleti Zamani & Marusik, 2020 [Araneae, Agelenidae]
Plexippus sengleti Logunov, 2021 [Araneae, Salticidae]
Saitis sengleti (Metzner, 1999) [Araneae, Salticidae]
Sengletiola Zoia & Rampini, 1994 [Coleoptera, Leiodidae]
Sengletus Tanasevitch, 2008 [Araneae, Linyphiidae]
Stenus sengleti Puthz, 1971 [Coleoptera, Staphylinidae]
Tetartopeus sengleti Bordoni, 1984 [Coleoptera, Staphylinidae]
Tychus sengleti Besuchet & Sabella, 1999 [Coleoptera, Staphylinidae]

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A new species of *Anguliphantes* Saaristo & Tanasevitch, 1996 from southern Tadjikistan, Central Asia (Araneae: Linyphiidae)

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Abstract: A new species, *Anguliphantes tadjik* sp. nov., is described from medium altitudes in the mountains of the Republic of Tadjikistan. The species is very similar to the Himalayan *A. nepalensis* (Tanasevitch, 1987) and *A. nepalensoides* Tanasevitch, 2011, but clearly differs by certain structural details of the palp in the male and by the shape of the scapus in the female.

Keywords: Taxonomy - spiders - Micronetinae - montane fauna.

INTRODUCTION

Anguliphantes Saaristo & Tanasevitch, 1996 is a small Eurasian micronetine genus currently containing 16 species (World Spider Catalog, 2021). At present only two species of this genus are known from the mountains of Central Asia: *A. nepalensis* (Tanasevitch, 1987) and *A. nepalensoides* Tanasevitch, 2011. *Anguliphantes nepalensis* was described from both sexes from the Himalayas of Pakistan, Nepal and India (Tanasevitch, 1987, 2011; Tanasevitch & Saaristo, 2006), while *A. nepalensoides* is only known from a single male from the Himalayan part of West Bengal, India (Tanasevitch, 2011).
Below I report on a third, new species of *Anguliphantes* with very close ties to both Himalayan congeners.

MATERIAL AND METHODS

This paper is based on specimens (belonging to a new species) from the author's personal collection which will be deposited in the Muséum d'histoire naturelle, Geneva, Switzerland (MHNG) and on comparative specimens in the Zoological Museum of Moscow University (ZMMU). Sample numbers are given in square brackets. Specimens preserved in 70% ethanol were studied using an MBS-9 stereomicroscope. Drawings were done with the help of a drawing tube; a Levenhuk C-800 digital camera was used for taking photographs. Leg chaetotaxy is presented in a formula, e.g., TiI: 2-1(2)-1-0, which means that tibia I has two dorsal spines, one or two prolateral, one retrolateral and no ventral spines, the apical spines are disregarded. The sequence of leg segment measurements is as follows: femur + patella + tibia + metatarsus + tarsus.
All measurements are given in mm. Scale lines in the figures correspond to 0.1 mm unless indicated otherwise. Figure numbers are given above the corresponding scale lines, the length they represent is given below them. The terminology of copulatory organs mainly follows that of Saaristo & Tanasevitch (1996).

Abbreviations

a.s.l.	above sea level
DS	distal part of scapus
EP	embolus proper
Fe	femur
FG	Fickert's gland
LC	lamella characteristica
LE	lateral extention of embolus
LL	lateral lobe of distal part of scapus
LO	lateral outgrowth of scapus
MA	membranous area of radix
MM	median membrane
Mt	metatarsus
P	paracymbium
PMP	posterior median plate
Ps	proscapus (= proximal part of scapus)
R	radix
SE	swollen extention of paracymbium
SS	serrate surface of embolus
St	stretcher
TA	terminal apophysis

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Ti tibia
TmI relative position of trichobothrium on the metatarsus of leg I

TAXONOMY

Anguliphantes Saaristo & Tanasevitch, 1996

Anguliphantes tadjik sp. nov.

Figs 1-9, 14-16

Holotype: MHNG; male; TADJIKISTAN, Sanglak Mts, Khatlon Region, Danghara District, environs of Sebiston, ca 38.248°N, 69.245°E, 1200-1500 m a.s.l.; 6.V.1991; leg. S. Ovtchinnikov.

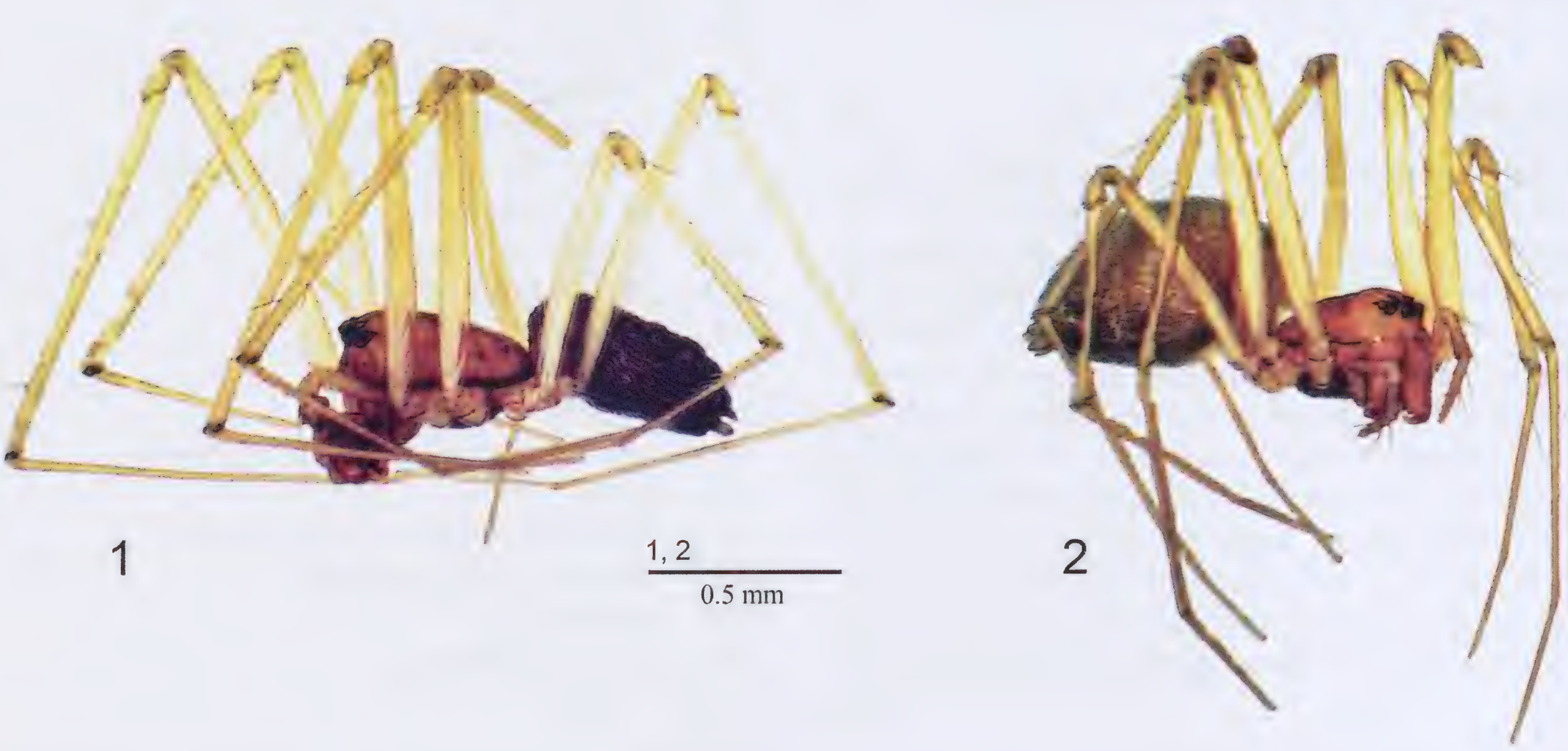
Paratype: MHNG; 1 female; collected together with the holotype.

Comparative material: *Anguliphantes nepalensis* (Tanasevitch, 1987): ZMMU (# Ta-8182); 1 male; NEPAL, Mustang District, Thakkhola, Chadziou-Khola, 2700-2900 m a.s.l., monsoon-influenced, dense, primary broadleaved forest in canyon, with bamboo growth; X.1969; leg. J. Martens. – ZMMU (# Ta-8183); 2 males, 3 females [sample #108]; Solukhumbu District, Khumbu, Mt. Everest region, 3250-3300 m a.s.l., confluence of Imja and Phunki-Drangka, *Betula* forest; 30.IX.-2.X.1970; leg. J. Martens.

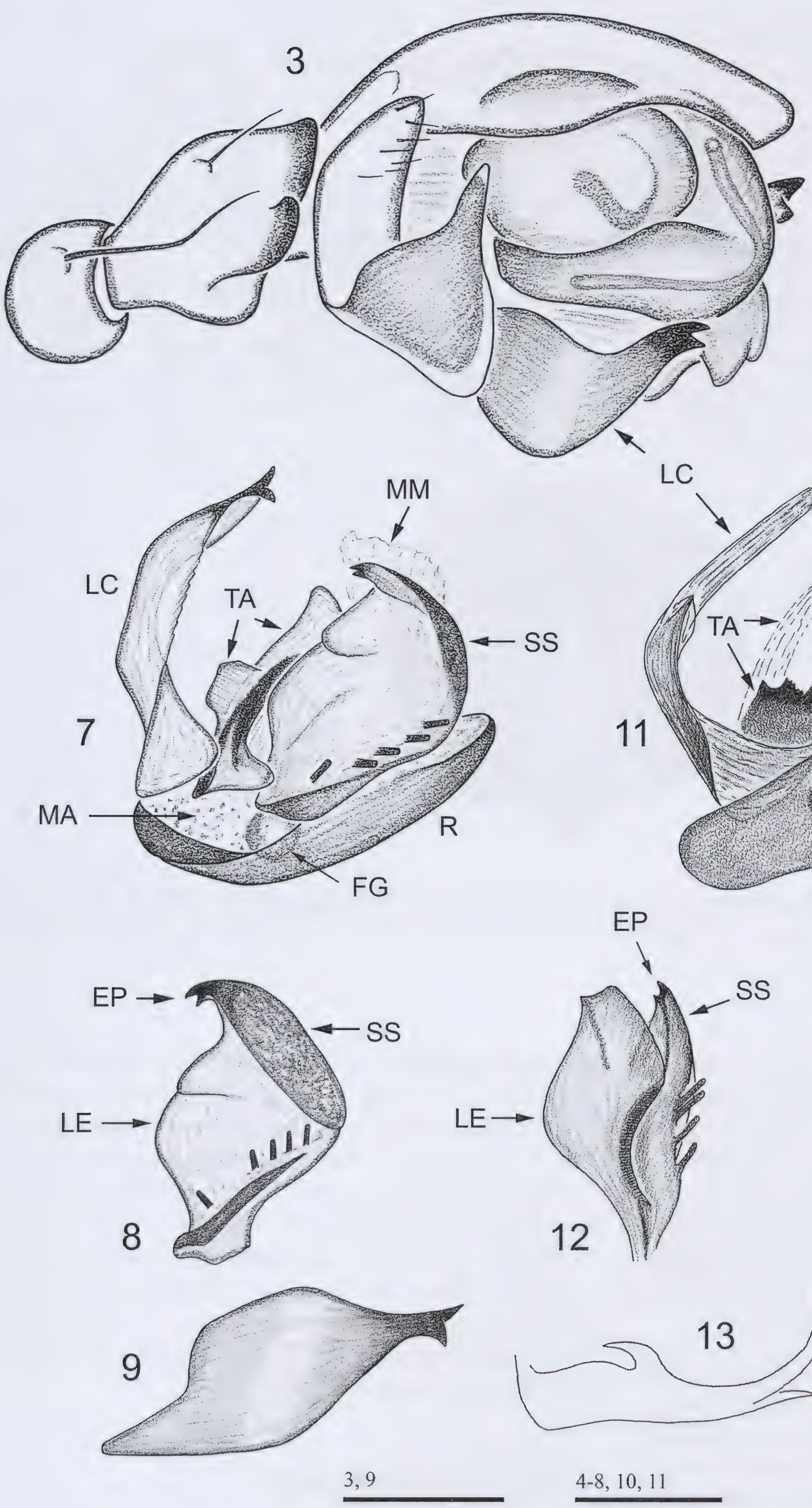
Etymology: The species name is a noun in apposition, meaning a native of Tadjikistan.

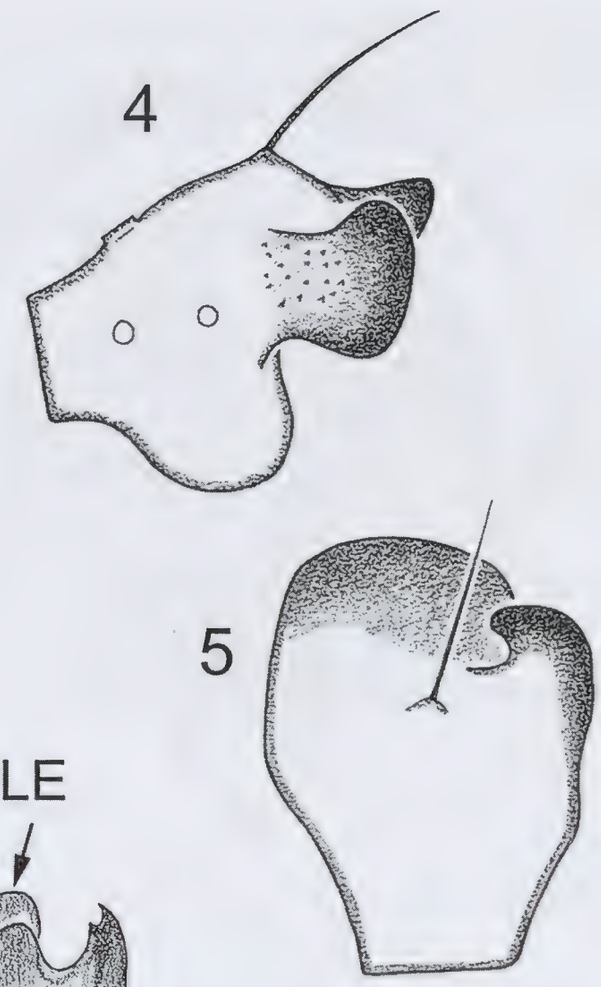
Diagnosis: The new species is distinguished from all known congeners by its relatively long legs. The male is also characterized by a modified palpal tibia, as well as by the shape of its lamella characteristica and of its embolus. The female differs by the shape of the proscapus base.

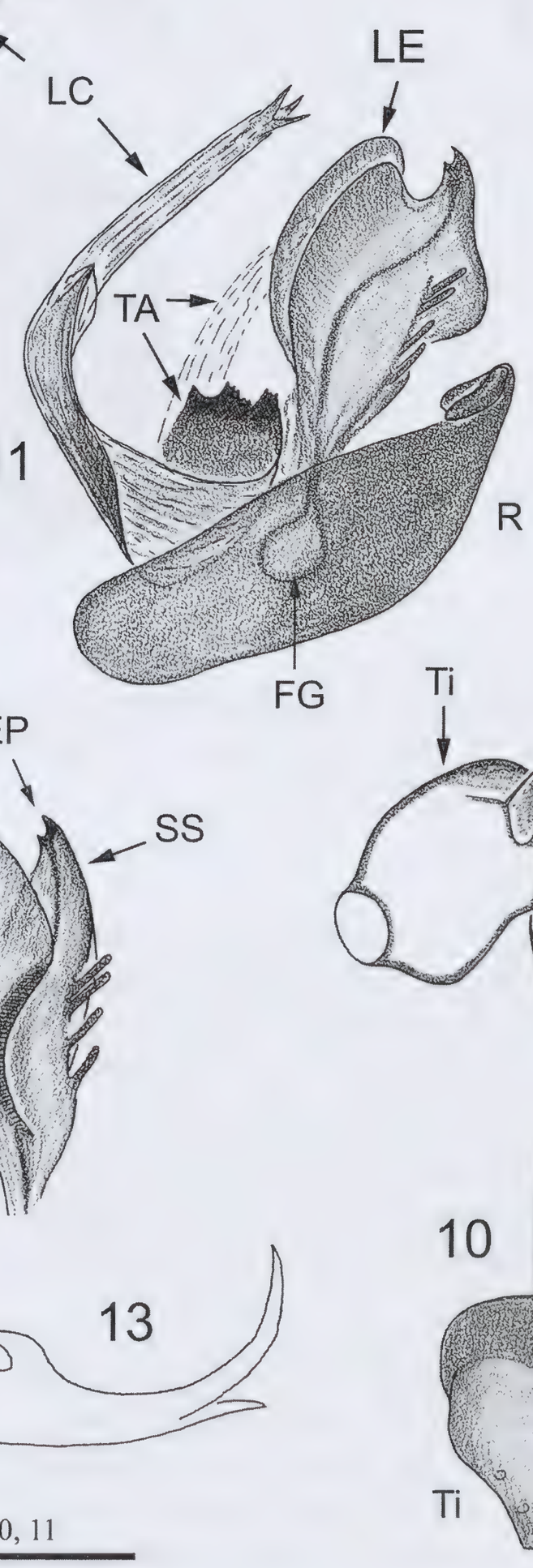
Description: *Male holotype*. Habitus as in Fig. 1. Total length 2.13. Carapace unmodified, 0.98 long, 0.85 wide; pale brown, with an indistinct grey, median spot and a greyish margin. Eyes relatively small, each with a black fringe. Chelicerae unmodified, 0.43 long, of same colour as carapace. Legs yellow to pale yellow. Leg I 7.42 long (1.75 + 0.30 + 2.00 + 1.98 + 1.39), leg IV 6.09 long (1.63 + 0.28 + 1.65 + 1.75 + 0.78). Chaetotaxy: FeI: 0-2-0-0, FeII-IV: 0-0-0-0; TiI: 2-1-1-0, TiII: 2-0-1-0; TiIII-IV: 2-0-0-0; MtI-III: 1-0-0-0, MtIV: 0-0-0-0. Metatarsi I-III each with a trichobothrium. TmI 0.08. Palp (Figs 3-9): Patella with a special spine (see Saaristo & Tanasevitch, 1996). Cymbium with neither posterodorsal outgrowth nor process. Tibia with a small, conical dorsal tubercle carrying a weak spine, and with a small arcuate projection retrolaterally. Paracymbium relatively large, toothless, its posterior and anterior pockets merged into a single large pocket. Terminal apophysis relatively small, complex in shape. Lamella characteristica widened near middle, narrowing distally, bifid apically. Embolus large and wide, its serrate surface (see Saaristo & Tanasevitch, 1996) well-developed. Five small, slender, blunt teeth at base of embolus. Embolus proper short, bifid. Abdomen (Fig. 1) 1.10 long, 0.65 wide, dark grey, dorsal pattern absent.
Female paratype. Habitus as in Fig. 2. Total length 2.35. Carapace unmodified, 1.05 long, 0.75 wide; yellow, with a grey median spot and a greyish margin. Eye sizes as in male. Chelicerae 0.45 long. Legs yellow. Femur and patella I 1.75 and 0.30 long, respectively, other segments of leg I missing. Leg IV 6.01 long (1.70 + 0.28 + 1.63 + 1.60 + 0.80). Chaetotaxy: FeI: 0-2(3)-0-0, FeII-IV: 0-0-

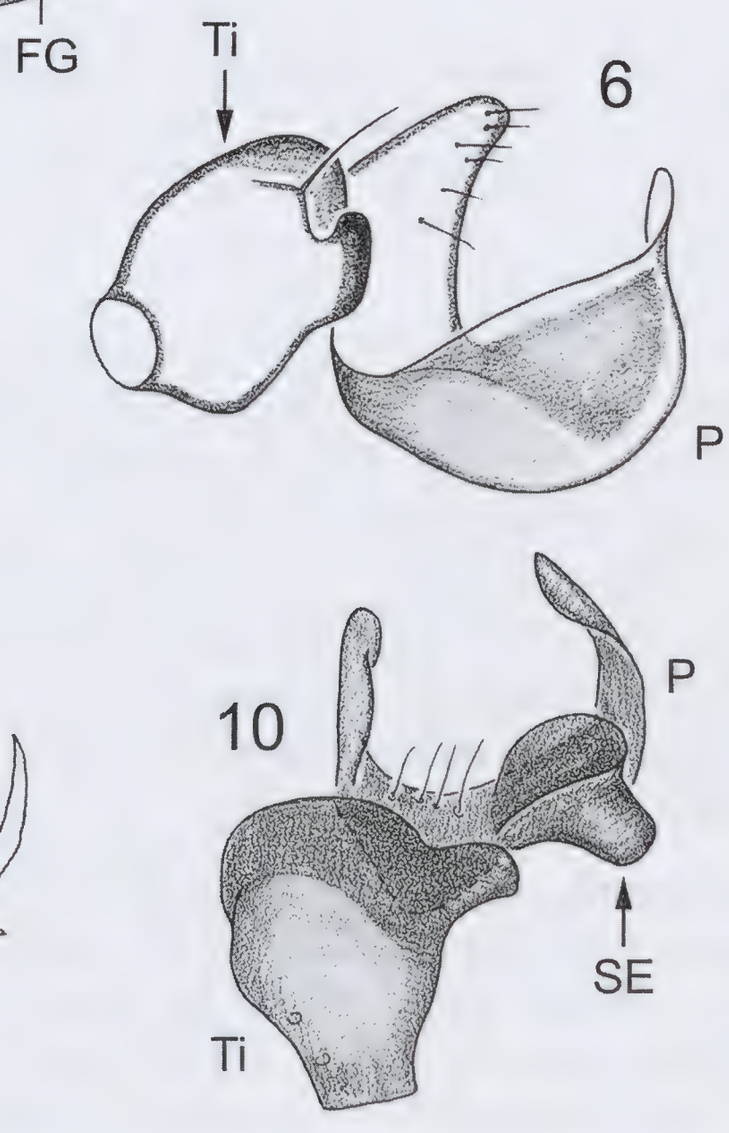


Figs 1-2. Photographs of the male holotype (1) and of the female paratype (2) of *Anguliphantes tadjik* sp. nov. (1) Habitus, lateral view. (2) Habitus, anterolateral view.

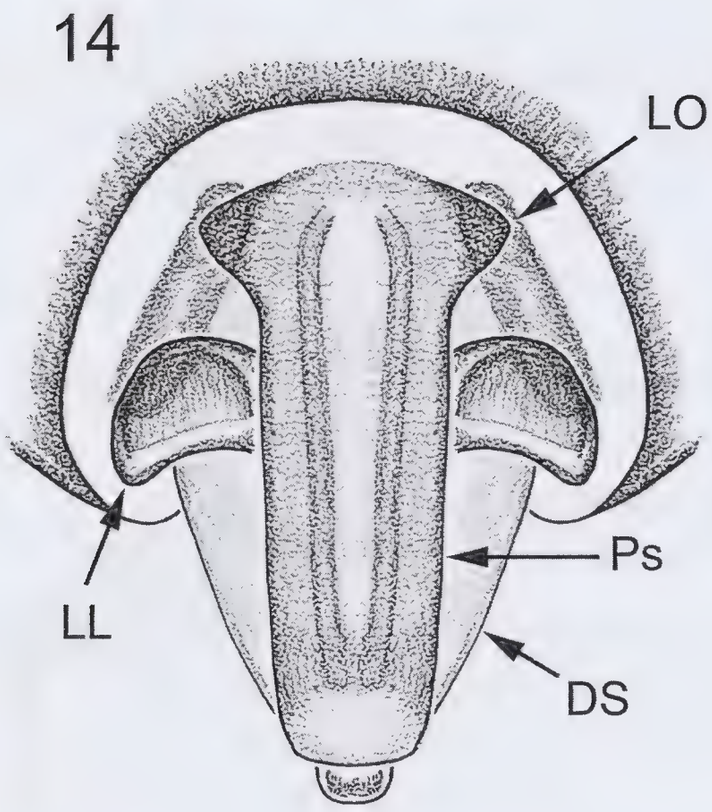


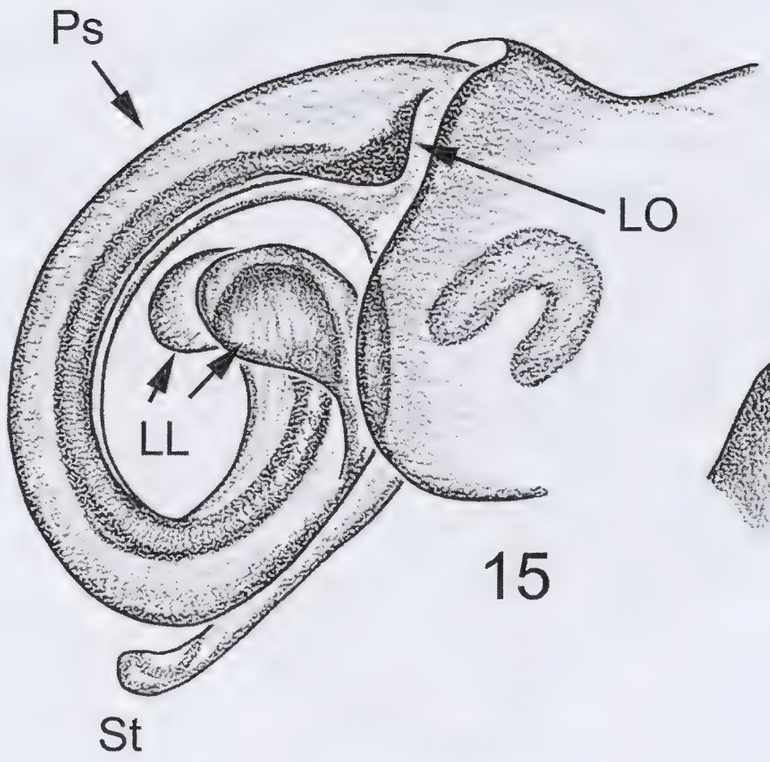


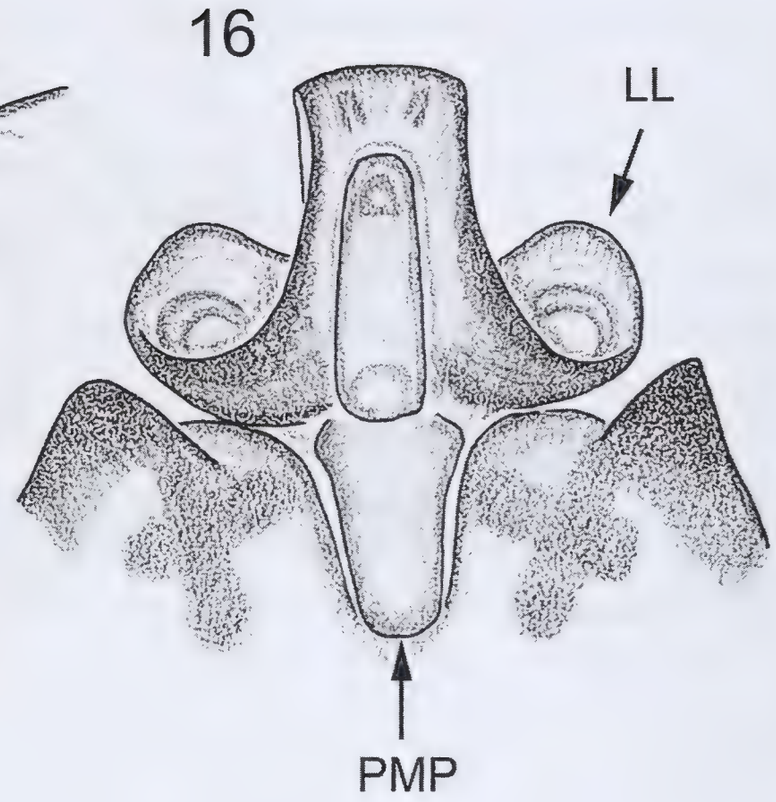


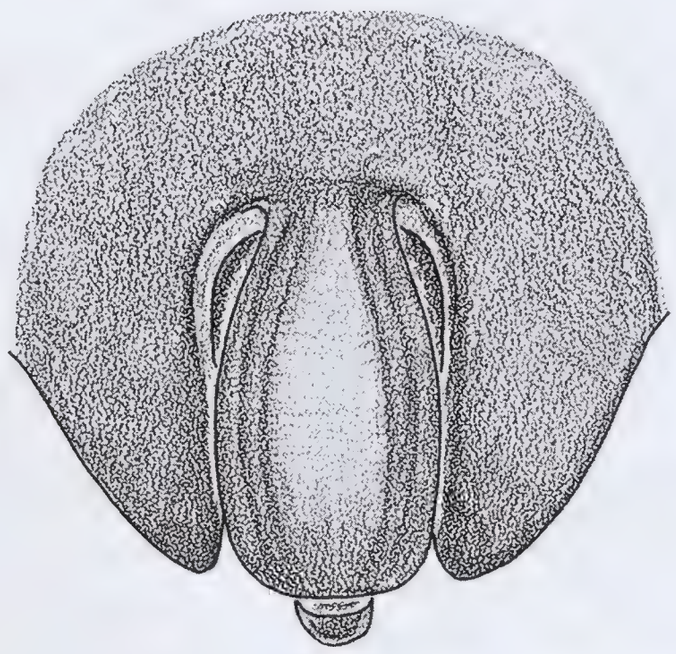


Figs 3-13. Details of the right palp of the male holotype of *Anguliphantes tadjik* sp. nov. (3-9) and of the male paratype (SMF # 34738) of *A. nepalensis* (Tanasevitch, 1987) from Pare, Nepal (10-13; reproduced from Tanasevitch & Saaristo, 2006). (3) Distal part of palp, retrolateral view. (4-5) Palpal tibia, lateral and dorsal views, respectively. (6, 10) Palpal tibia and paracymbium, retrolateral and dorsal views, respectively. (7, 11) Embolic division, lateral view. (8, 12) Embolus, lateral view. (9, 13) Lamella characteristica, lateral view.









14-17

Figs 14-17. Epigyne of female paratype of *Anguliphantes tadjik* sp. nov. (14-16) and of female paratype (SMF # 34738) of *A. nepalensis* (Tanasevitch, 1987) from Pare, Nepal (17; reproduced from Tanasevitch & Saaristo, 2006). (14, 17) Ventral view. (15) Lateral view. (16) Dorsal view.

0-0; TiII: 2-0-1-0; TiIII-IV: 2-0-0-0; MtII: 1(2)-0-0-0, MtIII: 1-0-0-0, MtIV: 0-0-0-0. TmI unknown, metatarsi I missing. Abdomen (Fig. 2) 1.50 long, 1.00 wide, grey. Epigyne (Figs 14-16): Proscapus long and slender, gradually curving, with a small outgrowth at its base on both sides. Distal part of scapus widening. Lateral lobes long, extending far out from both sides of proscapus. Stretcher long and slender, pit distinct. Posterior median plate small, longer than wide.

Taxonomic remarks: Judging from the modified palpal tibia, the structure of the embolic division in the male and the shape of the scapus in the female, the new species seems to be most closely related to the Himalayan *A. nepalensis* (see Introduction). *Anguliphantes tadjik* sp. nov. differs by the shape of the retrolateral projection of its palpal tibia (Figs 4-5 cf. Fig. 10), by the the absence of a swollen extension on its paracymbium (Fig. 6 cf. Fig. 10), by the shape of its embolus (Fig. 8 cf. Fig. 12), as well as by the shape of its lamella characteristica (Fig. 9 cf. Fig. 13). The female differs from that of *A. nepalensis* by the longer proscapus and the presence of lateral extensions on both sides of the proscapus (Fig. 14 cf. Fig. 17).

Breitling (2019, 2021) suggested that *Anguliphantes* is a junior synonym of *Oryphantes* Hull, 1932 on the basis of DNA barcoding data using a fragment of the MT-CO1 (cytochrome c oxidase subunit I) gene. However, it is well known that CO1 barcoding alone is quite unreliable at the generic level (for details see paragraph 7 at https://wsc.nmbe.ch/faq). The separation of the genera *Anguliphantes* and *Oryphantes* was confirmed by clear-cut differences in the genital structures of both sexes, in particular the embolus division of the male palp and the lateral walls of the female epigyne (for details see Saaristo & Tanasevitch, 1996).

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Two new species of myrmecophilous Pselaphinae from China (Coleoptera, Staphylinidae)

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Abstract: Two new myrmecophilous species of the supertribes Clavigeritae and Batrisitae are described from Yunnan, Southwest China: *Diartiger jiquanyui* **sp. nov.** associated with *Lasius* Fabricius ants, and *Myrmicophila yulong* **sp. nov.** associated with *Myrmica* Latreille ants. Both species are compared with and separated from related congeners, and images of their habitus and major diagnostic features are provided.

Keywords: Myrmecophile - new species - *Diartiger* - *Myrmicophila* - Yunnan.

INTRODUCTION

Our knowledge of the taxonomic and ecological diversity of myrmecophilous Pselaphinae in China has been continuously increasing during the past decade. A number of new genera and dozens of new species belonging to the supertribes Euplectitae, Goniaceritae, Pselaphitae, and especially Clavigeritae and Batrisitae were described from various areas of the country (*e.g.*, Yin *et al.*, 2010a-c, 2011a-c, 2012a-d, 2013, 2015a, b; Yin & Li, 2012, 2013a-c, 2014, 2015; Zhao *et al.*, 2010; Jiang & Yin, 2016, 2017; Yin, 2017a, b, 2018a, b; Yin & Lin, 2020; Yin & He, 2020). So far, the Chinese fauna of the obligate myrmecophilous supertribe Clavigeritae is represented by seven genera and 15 species, with the genus *Diartiger* Sharp being the most diverse group, containing seven species (Nomura, 1997; Li *et al.*, 2019; Yin & He, 2020). In China, members of *Diartiger* are most commonly found in the association with *Lasius* ants, and occasionally, also with *Ectomomyrmex* ants which often nest under stones or in decomposing logs. On the other hand, among the many recently described myrmecophiles belonging to the supertribe Batrisitae, the genus *Myrmicophila* Yin & Li is of particular interest regarding its distributional pattern and biology. Currently there are two species confined to the southwestern Chinese provinces of Yunnan and Xizang (Yin *et al.*, 2011b; Yin, 2021), which were collected only with *Myrmica* ants.

In May 2021 our colleague Quan-Yu Ji conducted a field trip in Yunnan, and collected a small series of pselaphines directly from ant nests in two localities. An examination of this material revealed two new species of *Diartiger* and *Myrmicophila*, which are described here.

MATERIAL AND METHODS

The type material of the new species described in this paper is deposited in the Insect Collection of Shanghai Normal University, Shanghai, China (SNUC). The text of the specimen label is quoted verbatim in quotation marks (‘’).

Dissected parts were preserved in Euparal on plastic slides that were placed on the same pin with the specimen. The habitus images of the beetle and host ant, as well as the ant’s full-face image was taken using a Canon 5D Mark III camera in conjunction with a Canon MP-E 65 mm f/2.8 1-5X Macro Lens, and a Canon MT-24EX Macro Twin Lite Flash was used as the light source. Images of the morphological details were produced using a Canon G9 camera mounted to an Olympus CX31 microscope under reflected or transmitted light. Zerene Stacker (version 1.04) was used for image stacking. All images were optimized and grouped into plates using Adobe Photoshop CC 2018.

The abdominal tergites and sternites are numbered following Chandler (2001) in Arabic (starting from the first visible segment) and Roman (reflecting true morphological position) numerals, *e.g.*, tergite 1 (IV), or sternite 1 (III).

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TAXONOMY

Diartiger jiquanyui sp. nov.

Figs 1A, 2

Type material: HOLOTYPE; ♂; CHINA, 'China: Yunnan, Deqin County, Yubeng Vill., 28°25'28.40"N, 98°48'38.89"E, ca. 2740 m, 8.iv.2021, Q.-Y. Ji leg., 云南德钦县云岭乡雨崩村' (SNUC). PARATYTYPE; 1 ♂; CHINA, same collection data as of holotype (SNUC).

Diagnosis: Body length approximately 2.4 mm. Anterior margin of clypeus broadly rounded. Antennomere 4 2.3 times as long as 3. Mesotrochanter with large curved ventral spine; mesofemur with blade-like ventral projection split into two lobes; mesotibia with row of denticles along mesal margin. Median lobe of aedeagus clearly separated into apical and basal parts.

Description: Male (Fig. 1A). Body length (combined length of head, pronotum, elytra and abdomen) 2.41-2.42 mm, colour reddish-brown.

Fig 1. Dorsal habitus of two new species: (A) *Diartiger jiquanyui* sp. nov. (B) *Myrmicophila yulong* sp. nov. Scale bars: 0.5 mm in A, 1 mm in B.

Head (Fig. 2A) elongate, length from anterior margin of clypeus to posterior margin of head (excluding neck region) 0.51-0.52 mm, width across eyes 0.29 mm; clypeus with broadly-rounded anterior margin; each eye composed of approximately 25 facets; antenna clubbed, with short antennomere and 2 and elongate 3 and 4 (Fig. 2B), length of antennomere 2 0.05-0.06 mm, 3 0.16-0.17 mm, 4 0.38-0.39 mm; antennomere 4 longest, narrowed at base and broadly apically, truncate at apex, approximately 2.3 times as long as 3; distinct gular foveae (posterior tentorial pits) close, in shared impression.

Pronotum (Fig. 2A) subglobose, surface roughly punctate, approximately as long as wide, length along midline 0.44-0.45 mm, maximum width 0.43-0.44 mm; widest at middle; with distinct median antebasal impression.

Elytra much broader than long (Fig. 1A), length along suture 0.64-0.65 mm, maximum width 0.86-0.87 mm; with linear microsculpture on disc, and long setae

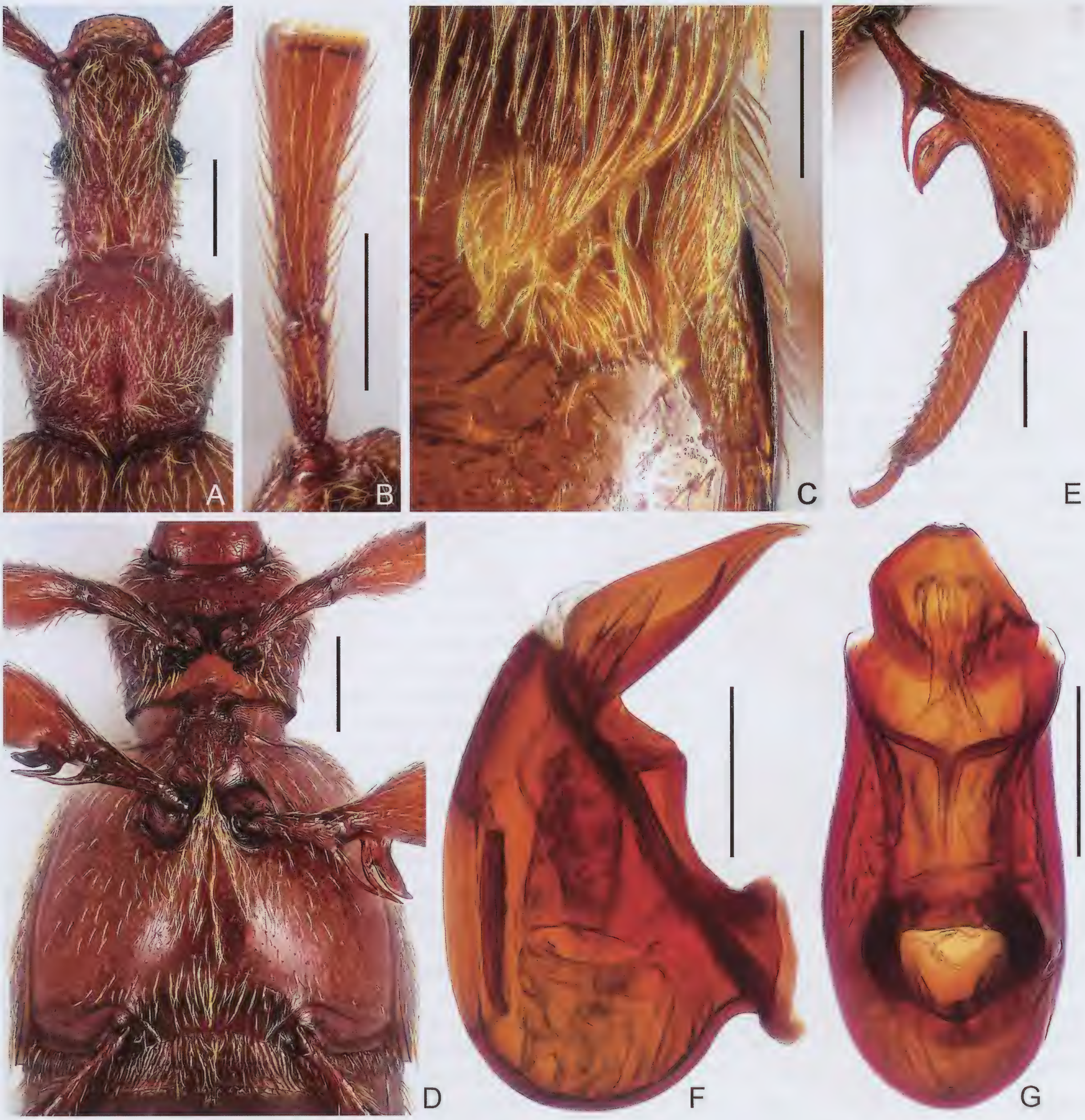

Fig 2. Diagnostic characters of *Diartiger jiquanyui* sp. nov. (A) Head, pronotum, and elytral base. (B) Left antennomeres 2-4. (C) Trichomes on elytral and abdominal bases. (D) Prosternum and meso- and metaventrites. (E) Mesotrochanters, mesofemur and mesotibia. (F, G) Aedeagus, in lateral (F), and ventral (G) view. Scale bars: 0.2 mm in A, B, D, E; 0.1 mm in C, F, G.

along posterior margin; posterolateral margins with sub-triangular tufts of setae (Fig. 2C). Metathoracic wings fully-developed. Prosternum (Fig. 2D) roughly sculptured medially; mesoventrite (Fig. 2D) with short intercoxal ridge, metaventrite (Fig. 2D) convex admesally, both ventrites with dense, thick setae along midline, with distinct linear microsculpture laterally.
Fore and hind leg simple; middle leg (Fig. 2E) greatly modified, mesotrochanter with long, sharp, and curved ventral spine, mesofemur with broad blade-like projection separated into two lobes, mesotibia moderately expanded at basal 1/3, with row of denticles of various size along mesal margin.
Abdomen large, slightly broader than long, length along midline 0.80-0.82 mm, maximum width 0.84-0.87 mm; composite tergite broadly and deeply concave mediobasally, with ball of trichomes (Fig. 2C) at basolateral region, first pair of paratergites (Fig. 2C) with linear trichomes.
Aedeagus (Fig. 2F, G) strongly sclerotized, length 0.35 mm; basal capsule with large basoventral projection, median lobe gradually narrowing apically, with small membranous structure at apex.
Female. Unknown.

Comparative notes: *Diartiger jiquanyui* sp. nov. differs from all known congeners from China by the broad, blade-shaped and deeply split projection of mesofemora, rowed denticles along the mesal margin of mesotibiae, as well as the median lobe of aedeagus clearly separated into two parts. In China, only *D. songxiaobini* (Yin & Li) from West Tianmu Mountain, Zhejiang, eastern China has a similarly structured aedeagus (Yin *et al*., 2010b), but in the latter species the forms of the spines of the middle legs are quite different.

Distribution: China: Yunnan.

Host ant: *Lasius* sp. (Fig. 4A-C).

Etymology: The new species is named after Quan-Yu Ji, the collector of the holotype.

Myrmicophila yulong sp. nov.

Figs 1B, 3

Type material: HOLOTYPE; ♂; CHINA, 'China: Yunnan, Lijiang City, Yulong Snow Mt., Lanyue Valley, 27°7'46.49"N, 100°14'30.14"E, ca. 2900 m, 29.iii.2021, Q.-Y. Ji leg., 玉龙雪山蓝月谷' (SNUC). PARATYPE; 1 ♀; CHINA, same collection data as of holotype (SNUC).

Diagnosis: Body length slightly over 3.5 mm. Antennomere 5 greatly extended mesally, 6 moderately transverse, 8-10 moniliform, successively broader. Mesotibia with distinct apical spur, slightly sinuate along mesal margins; metafemur broadly expanded on dorsal margins. Aedeagus with median lobe greatly extended apically and strongly curved ventrally.

Description: Male (Fig. 1B). Habitus stout, length (combined length of head, pronotum, elytra and abdomen) 3.66 mm, colour uniformly reddish-brown; dorsal surface of whole body finely punctate, with short recumbent setae on elytra and abdomen slightly denser than those on head and pronotum.
Head (Fig. 3A) sub-rectangular at base, length from anterior margin of clypeus to posterior margin of head (excluding neck region) 0.66 mm, width across eyes 0.69 mm; distinct asetose vertexal foveae at level of posterior margin of eyes; mediobasal ridge extending from posterior margin of head towards approximately posterior 1/3 of head length; frons broadly and shallowly impressed between moderately raised antennal tubercles; postocular margin angularly rounded; eyes moderately prominent, each composed of approximately 50 facets. Antenna elongate, lacking distinct club, length 1.70 mm; antennomere 1 (scape) thick, with deep dorso-ventral notch at apex, 2 and 3 much narrower than 1, elongate, successively broader and longer, 4 broader than 3, slightly transverse, 5 (Fig. 3B) transverse, strongly expanded on mesal margin, 6-10 moniliform, 6 broader than 7, 7 and 8 of similar width, 9 broader than 8, 9-10 gradually broader, 11 subconical, approximately as broad as 10. Gular area with foveae (posterior tentorial pits) close to each other, in shared oval impression, with thin gular ridge extending to mouthparts.
Pronotum (Fig. 3A) sub-globose, widest at anterior 2/5, length along midline 0.7 mm, maximum width 0.72 mm, with round lateral margins gradually narrowing from broadest point towards base and apex, anterior and posterior margin almost straight; with short median longitudinal sulcus at base, and distinct asetose lateral antebasal foveae.
Elytra broader than long, length along suture 1.07 mm, maximum width 1.34 mm, each elytron with three large, nude basal foveae, sutural stria complete, with short and shallow discal stria, lacking marginal stria. Metaventrite strongly convex lateral to midline.
Legs moderately elongate; foreleg simple; mesotibia (Fig. 2C) with distinct spur at apex, mesal margin slightly sinuate; metafemur (Fig. 2D) broadly expanded along dorsal margin before middle.
Abdomen slightly broader than long, widest at tergite 1 (IV), length along midline 1.23 mm, maximum width 1.33 mm. Tergite 1 (IV) at mid-length slightly longer than 2 (V), tergites 1 (IV) to 3 (VI) successively shorter, tergite 4 (VII) approximately as long as tergite 2 (V).
Aedeagus (Fig. 2E, F) well-sclerotized, length 0.75 mm; median lobe with large, transverse basal capsule and foramen; ventral and dorsal lobe each composed of flattened, apically pointed and curved sclerites; parameres paired and weakly-sclerotized, attached to ventral side of capsule.

Fig 3. Diagnostic characters of *Myrmicophila yulong* sp. nov. (A) Head, pronotum. (B) Right antennomeres 5-11. (C) Mesotibia. (D) Metafemur. (E, F) Aedeagus, in dorsal(E) and ventral (F) view. Scale bars: 0.5 mm in A, D; 0.4 mm in B; 0.3 mm in C; 0.2 mm in E, F.

Female. External morphology similar to male; antenna shorter and unmodified; mesotibia lacking spur at apex, metafemur lacking expansion. Measurements (as for male): body length 3.59 mm, length/width of head 0.65/0.71 mm, pronotum 0.73/0.75 mm, elytra 1.35/1.04 mm, abdomen 1.17/1.37 mm, length of antenna 1.62 mm, each eye with approximately 40 facets.

Comparative notes: Two species of *Myrmicophila* have been known: *M. tangliangi* Yin & Li from Yunnan (Yin *et al*., 2011b) and *M. motuoensis* Yin from Xizang (Yin, 2021), each was collected from nests of a different *Myrmica* species. The new species is in general similar to *M. tangliangi* and *M. motuoensis* by sharing identical positions of the male sexual characters on antennomeres 5 and metafemora, indicating close relationships between these three species. However, a number of characters, both external and internal, support the status of a distinct species of the population from Yulong Mountain. The development of the male antennomeres of *M. yulong* sp. nov. appears to be intermediate between *M. tangliangi* and *M. motuoensis*, the antennomeres 5-7 of the new species are relatively much broader than *M. tangliangi*, but narrower than those of *M. motuoensis*; the mesotibia is slightly sinuate along the mesal margin, but they are evenly

Fig 4. Hosts of *Diartiger jiquanyui* sp. nov. (A-C) and *Myrmicophila yulong* sp. nov. (D-F). (A, D) Habitus, dorsal. (B, E) Same, lateral. (C, F) Full face view. Scale bars: 1.0 mm in A, B, D, E; 0.5 mm in C, F.

slightly curved in *M. tangliangi* and *M. motuoensis*; the apical spur of mesotibia is much larger than that of *M. motuoensis*, and of similar size but of a different shape as in *M. tangliangi* (triangular, blade-like); and the median lobe of the aedeagus is more greatly extended apically and more strongly curved ventrally than the other two species. In addition, the validation of the new species is also supported by ecological evidence. The ant host of *M. yulong* sp. nov. is morphologically more similar to that of *M. motuoensis* from Motuo, Xizang, but apparently represents a different species by the smaller body size, and presence of a distinct reversed V-shaped sulcus on the pronotal disc (sulcus vague in *Myrmica* sp. from Muotuo).

Distribution: China: Yunnan.

Host ant: *Myrmica* sp. (Fig. 4D-F).

Etymology: The new species is named after its type locality, the Yulong Snow Mountain.

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Bats (Mammalia, Chiroptera) from a cave area in NW Italy

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Abstract
Caves play an important role in bat ecology, offering natural roosting and wintering sites. In the reproductive period, bats need to find an effective foraging environment away from the cave entrance, but only few studies have considered the use of foraging habitats in the immediate proximity of the caves. We provide a list of 18 bat species and 5 bat acoustic groups observed in a system of 81 caves in NW Italy. Winter censuses carried out during 17 years showed an increase of the Greater Horseshoe bat, a species of conservation concern. In the summer period this rare species was also observed foraging in nearby areas. Recording of bat calls in the summer period was performed both at cave entrances and in three foraging habitats present in the area surrounding the cave (woods, agricultural mosaic with artificial light, dark mosaic). Light mosaics and woods showed the highest foraging activity (160.3 and 72.0 pass/hour), while woods and cave entrances were accessed by the largest number of bat species. Our survey improves the inventory of bat species in a poorly sampled area, and we recommend a reduced tourism access, thereby promoting preservation of bats.

Keywords: Monte Fenera karst caves - *Rhinolophus ferrumequinum* - Vespertilionidae - extra-cave habitats.

INTRODUCTION

Although caves may be used by bats throughout all year (e.g. as thermally favourable breeding habitat), it is well known that their most important role in ecology of temperate bats is as hibernacula (Zukal *et al.*, 2017). However, even if there are a multitude of studies examining the presence of bats wintering in caves as part of bat monitoring programs (Loeb *et al.*, 2015; Collins, 2016), to date there are surprisingly few systematic investigations of bat activity in habitats nearby hypogeal sites compared to other habitats (Wieser *et al.*, 2020).
Hibernacula have a key role in the life cycle of bats (Altringham, 2011; Toffoli & Calvini, 2021) and the survival of many bat species worldwide depends on the availability of natural caves and other underground sites such as mines (Mickleburgh *et al.*, 2002) that provide relatively stable above-freezing temperature and high humidity (Zukal *et al.*, 2017). Subterranean winter temperatures are warmer and less variable further from the surface (McClure *et al.*, 2020) and are close to the mean annual surface temperature for the nearby area (Zukal *et al.*, 2017). Furthermore, hibernaculum humidity impacts overwinter survival since dry conditions may lead to reduced length of torpor bouts (Thomas & Geiser, 1997) and may stimulate arousals (Ben-Hamo *et al.*, 2013; Klüg-Baerwald & Brigham, 2017), increasing death probability. Highly stable climate conditions in caves thus promote energy-saving torpor and enable hibernating bats to overcome cold winters (McClure *et al.*, 2020; Speakman & Thomas, 2003).
Identifying and protecting hibernacula is crucial for bats conservation (Glover & Altringham, 2008) and their numbers and diversity in hypogeal environments are influenced by many factors including human disturbance, cave dimensions, structural complexity and microclimate, availability of food in the surrounding landscape, parasite and predation pressure. Historical use by bats and maneuverability of flight and interactions between species have a relevant impact on roost selection as well (Furey & Racey, 2015). Intraspecific needs and tolerance may vary geographically (Klüg-Baerwald & Brigham, 2017) and they also determine the suitability of a site. Selection of microclimate conditions by bats during hibernation is complex (McClure *et al.*, 2020) and not easily predictable.
External environments surrounding caves are equally important for bats all year round, even though foraging

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habitat preferences may vary among species. Forests provide cover for emerging bats reducing flight costs and predation risk (Verboom & Spoelstra, 1999; Coleman & Barclay, 2013) and represent a source of invertebrate prey (Kofoky *et al.*, 2006), whilst forest edges contribute to landscape connectivity enhancing the movement of species (Heim *et al.*, 2015). Scattered trees and hedgerow in farmland and prairie riparian areas harbour large numbers of insects and, consequently, they are used as foraging habitats (Lumsden & Bennett, 2005; Holloway & Barclay, 2000; Toffoli, 2016). In Mediterranean regions, wetlands constitute an essential ecosystem for bats and a higher bat foraging activity is reported near more accessible water bodies (Rainho, 2007). Anthropic environments are used by bats as well but, although they might be particularly attractive to *Pipistrellus*, *Eptesicus* and *Hypsugo* species, they are much less so to *Myotis* and *Plecotus* and they can even cause habitat fragmentation (Barataud, 2016).

While the study of the relationships between habitats and bat presence, or bat activity, has attracted much attention in a multitude of areas (Kunz & Fenton, 2003), the study of bat activity near the area surrounding the cave entrance has drawn little attention. We carried out systematic recordings of bat calls at cave entrance and three other habitat types (wood, dark open mosaic, open mosaic with light) to better understand the importance of these habitats for bats.

We examined the Monte Fenera Natural Park area, in NW Italy, which includes 81 caves (Lana & Sella, 1986). Previous biospeleological surveys conducted by Gruppo Speleologico Biellese C.A.I. (GSBi-CAI) from 1993 to 1999 reported the presence of Mouse-eared bats *Myotis myotis/blythii*, Lesser Horseshoe bats *Rhinolophus hipposideros* and Greater Horseshoe bats *Rhinolophus ferrumequinum* not only inside the major caves of the massif but also in several small cavities (Pascutto & Balestrieri, 2001). Further observations in subsequent

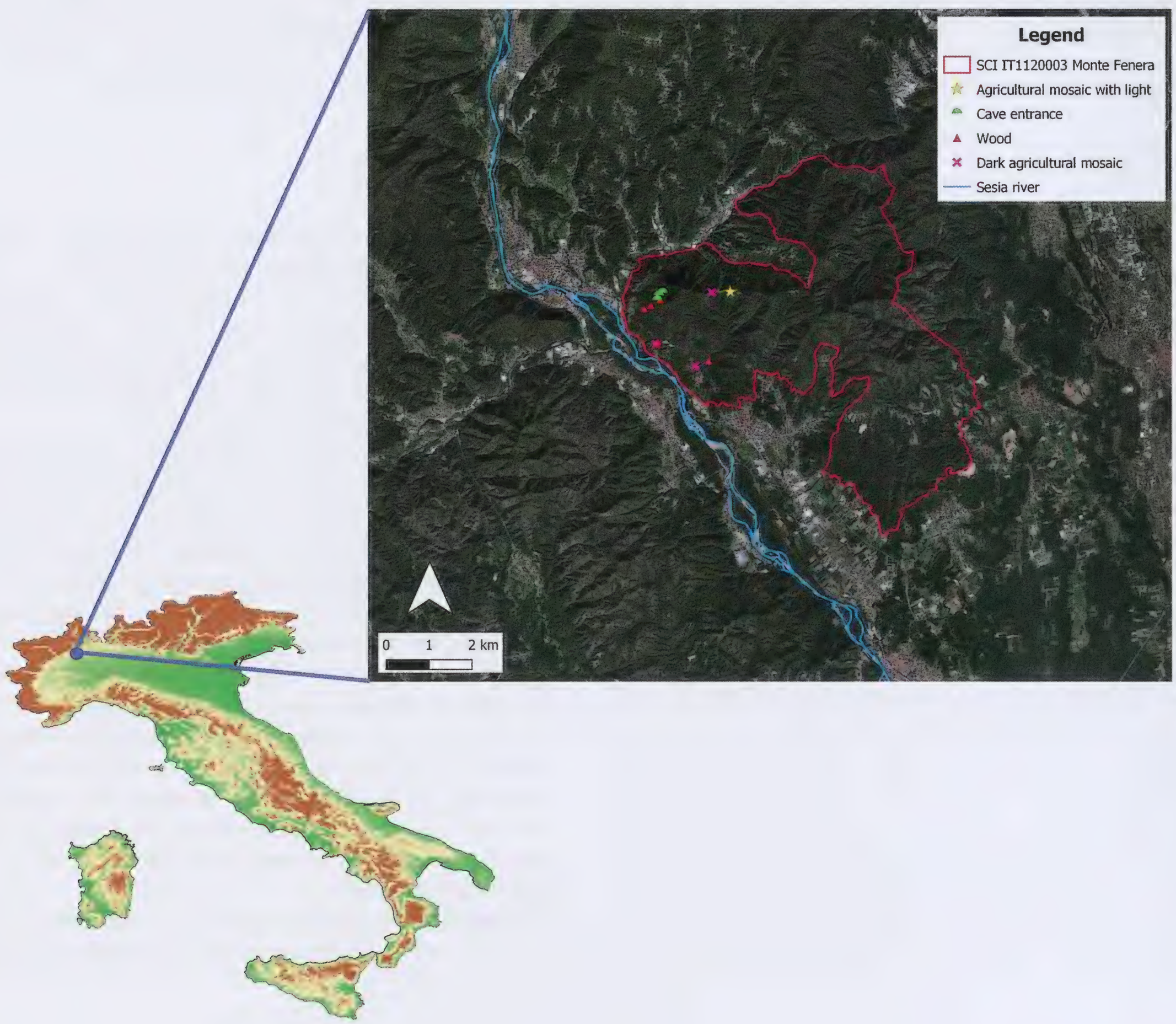

Fig. 1. Map of the study area in NW Italy. Star: sampled sites of the Fenera's caves area.

years confirmed this first list of species and revealed the attendance of a cave by Long-eared bats (Lana *et al.*, 2021). The availability of different habitat types nearby caves makes the area suitable as breeding, hunting or swarming sites not only for cave-dwelling bats, extremely favoured by the geological features of Monte Fenera, but for tree-dwelling bats as well.

Our study aims to fill the lack of data about bat fauna in this area by utilizing winter censuses carried out along a 17-year period, some captures with mist nets at cave entrance, several occasional reports, and an intense monitoring through bat call recordings collected in 12 sites pertaining to four habitat categories inside the Fenera area.

MATERIAL AND METHODS

Study Area

The Monte Fenera, in NW Italy, is a protected area of 3378 ha (Fig. 1), included in the Sites of Community Importance list (code IT1120003). Evidence of the use of the caves since the Riss-Würm interglacial was documented by the description of fossils of at least 9 species of bats (Berto *et al.*, 2016). Our sample sites are comprised in the municipalities of Borgosesia, Valduggia and Grignasco. Most of the protected area is a carbonate-built hill that is home to 81 karstic caves at an altitude of 600-800 m a.s.l. The environment surrounding the caves' entrance is mainly composed of woods, with some cultivated areas and small villages from 2-3 km henceforth.

Winter areas

We inspected the four largest caves, namely:

- Bondaccia (Italian cave registry code PI2505); WGS84 45.7114438°N, 8.3118285°E, 690 m a.s.l., 500 m-long.
- Ciota Ciara (code PI2507); WGS84 45.7108912°N, 8.3112443°E, 675 m a.s.l., 202 m-long.
- Ciutarun (code PI2506); WGS84 45.710138°N, 8.3102257°E, 655 m a.s.l., 66 m-long.
- Arenarie (code PI2509); WGS84 45.711919°N, 8.3145207°E, 770 m a.s.l., 3 km-long.

Summer-autumn areas

We inspected the environment surrounding the Monte Fenera cave area, grouping the observations among four habitat categories:

- cave entrance: the sampling covers the space (about 20-30 m) in front of the entrance of three large caves, Bondaccia, Ciota Ciara and Ciutarun.
- woods: five sampling points. The woods are dominated by chestnut which is accompanied by other species such as ash, English oak, sessile oak, Turkey oak, birch, maple, aspen, wild cherry, willow, and mountain ash; black locust has invaded the southern hills, while in the humid valleys and along the streams there is alder and black poplar. To the north, on the cooler slopes, beech is abundant, while to the south, on rocky walls and calcareous soils, there is manna ash, a typical essence of Mediterranean environment to which butcher's broom and juniper also belong, which are found in abundance. Natural conifers (Scots pine) are present sporadically while the most common are those of planting, preferred by man for their rapid growth (such as strobe pine). Among typical shrubs in the woods are hazelnut, dogwood, elder, hawthorn, barberry and privet.
- agricultural mosaic with light: two sampling points. Open spaces with grass vegetation and orchards, with small buildings and the presence of light coming from the houses.
- dark agricultural mosaic: two sampling points. Open spaces with grass vegetation and orchards, with no buildings nor light.

Areas with incidental observations

We utilized some occasional data collected by speleologists in smaller caves:

- La Caudrola PI2735: WGS84 45.7045478°N, 8.3101146°E, 515 m a.s.l.
- Buco delle Marmitte della cava Antoniotti PI2550: WGS84 45.7006103°N, 8.312411°E, 402 m a.s.l.
- Buco delle Radici PI2540: WGS84 45.7116969°N, 8.3225534°E, 804 m a.s.l.
- Bell'ingresso PI2539: WGS84 45.7104921°N, 8.3242896°E, 754 m a.s.l.

Other data were collected from citizens reporting dead specimens, and in a single event placing mist nets at the Bondaccia cave entrance in October 2012.

Field surveys

Winter census

Hibernating individuals were monitored through standardized counts carried out in their underground roosts between the last five days of December and the first ten days of February (Battersby, 2010). Hibernation site surveys were repeated once every year at each site in order to minimize disturbance. Bats were counted directly or with binoculars along all human accessible tracts in caves, or with the aid of images in case of aggregated groups that required the use of photography or video cameras (Toffoli & Calvini, 2021).

Summer-autumn census

In our study area, the year-round reproductive life cycle of bats typically starts with the autumnal swarming-mating period, followed in spring and early-summer by a female-lactating period. In late summer, both adults and recently born bats can be observed foraging. In this study we inspected the environment utilized by foraging bats from early July to early October, thus encompassing both the lactating period and the periods when young bats start to forage independently, with some overlapping with the mating period.

Bat activity was investigated using AudioMoth bat detectors (Hill *et al.*, 2019), with their microphones placed 1.5 m above the ground. Real time recordings were made all-night-long at a sampling frequency of 256 kHz. We started bat acoustic sampling half an hour after sunset until half an hour before sunrise. This time interval includes the main peaks of activity for most insectivorous bats of the temperate zone (Erkert, 1982). Recordings were made on nights without precipitation, with wind strength below 6 m/s and temperature above 10 °C at sunset, to avoid measuring low bat activity due to weather factors. All recordings were then divided in segments of 5 sec duration using the Kaleidoscope program 3.1.1 (Wildlife Acoustics, Maynard, Massachusetts, USA).

To describe activity levels, the number of passes per hour of each different species and acoustic groups was used (Barataud, 2016). A pass is defined as a recording consisting of at least one echolocation signal (call) up to a total length of 5 sec (Thomas & West, 1989; Barataud, 2016). In the results, we reported the average number of bat passes / hour in order to take into account the difference in the number of sampled sites and the recording time in the different habitat categories.

Data analysis

Winter census

Population trend was analyzed with the TRIM software (Pannekoek & Van Strien, 2001) through the package "Rtrim" 2.0.6 within the R statistical environment (Bogaart *et al.*, 2016). TRIM implements log-linear Poisson regression models to analyse time series of count data (Gregory *et al.*, 2005), and was developed for the analysis of time series of counts with missing values (Pannekoek & van Strien, 2001). It has been utilized to analyze trends in hibernating bats (Uhrin *et al.*, 2010; Van der Meij *et al.*, 2015; Toffoli & Calvini, 2019).

Summer-autumn census

Species identification was obtained by analyzing each bat call sequence following the methodological approach provided by Barataud (2016) and comparing the data with those published by Russo & Jones (2002). The identification method is based on the signal shape (FM: frequency modulation; QCF: quasi constant frequency), the energy peak distribution and on the measurement of the following parameters: start frequency (SF), end frequency (EF), bandwidth (BW), frequency of maximum energy (FME) in kHz, duration (D) and inter-pulse interval in ms (IPI). To reduce the time spent examining sonograms, in a first step we utilized the Sonochiro® 3.3.2 software (Biotope Society, France) for automatic identification of echolocation signals of European bats (Azam *et al.*, 2015; Charbonnier *et al.*, 2016). This software identifies signals in a recorded sequence and classifies them at a homogeneous species group level according to characteristics of signals. The software attributes a reliability index from 0 to 10 for each identification. In a second step, we controlled manually all sequences with a score lesser than 5, as indicated by Toffoli & Rughetti (2017), to attribute sequences to one species or one acoustic group according to the characters reported in Barataud (2016), Russo & Jones (1999) and Middleton *et al.* (2014).

Signals belonging to the genus *Myotis*, excluding those classified at a specific level, were incorporated into the two groups *Myotis* LF (*Myotis myotis* and *Myotis blythii*) and *Myotis* HF (all other species), due to the difficulties encountered in identifying them at species level (Russo & Jones, 2002). Due to a lack of firm discrimination criteria for bioacoustic distinction between *Plecotus auritus*, *Plecotus austriacus* and *Plecotus macrobullaris*, we attributed all signals of the genus to the *Plecotus* sp. group.

With regard to *Pipistrellus kuhlii* and *Pipistrellus nathusii*, whose identification is difficult (Barataud, 2016), only sequences with a score equal to or greater than 9 were attributed to one of the two species. All others were controlled manually and only those with the characteristic social calls were identified at species level (Russo & Jones, 1999; Middleton *et al.*, 2014), while the remnants were referred to the acoustic group *Pipistrellus kuhlii/nathusii*.

Sequences with FME signals from 20 to 30 kHz and the presence of characteristic alternate FM/QCF and QCF signals of different FME were associated to the *Nyctalus* genus (Waters & Jones, 1995). Sequences of primarily FM/QCF signals either longer than 17 ms and with end frequency between 21 and 24 kHz, or shorter than 5 ms and with EF between 29 and 32 kHz were associated to *Eptesicus serotinus* (Barataud, 2016). Concerning the identification of European Free-tailed Bat *Tadarida teniotis*, in order to exclude *Nyctalus lasiopterus* and the social calls of *Nyctalus leisleri*, reference was made to the guidelines of Barataud (2016). In particular, in order to exclude *Nyctalus lasiopterus*, sequences without alternating structure between QFC and FM signals and with a maximum energy frequency between 9 and 13 kHz have been attributed to *Tadarida teniotis*, while as regard the exclusion with the social calls of *Nyctalus leisleri*, reference was made to the initial form of the characteristic signal of the social calls of *Nyctalus leisleri*.

RESULTS

Winter census

The winter censuses in the four largest caves of Fenera along the 17-years monitoring period confirmed the cumulated presence of 534 *Rhinolophus ferrumequinum* (501 at Bondaccia, 18 at Ciota Ciara, 11 at Arenarie, 4 at Ciutarun), while other species where much less abundant: 3 large *Myotis* (*M. myotis/blytii* at Bondaccia), 1 small *Myotis* (*M. alcatoe/brandtii/mystacinus* at Bondaccia), 1 *Myotis crypticus* and 1 *Pipistrellus* sp. at Ciota Ciara.

The trend of observed and estimated number of wintering *Rhinolophus ferrumequinum* is reported in Table 1, with a clear and steady increase of census individuals.
The TRIM population analysis model shows a significant overall gradient of 1.22 (Wald test; $p < 0.001$), which corresponds to an average annual increase of 22 % over the period considered (Fig. 2).

Table 1. Number of hibernating *Rhinolophus ferrumequinum* bats in Fenera caves, and trends (TRIM index, TRIM estimates and standard errors) along 17 winters. The dashes refer to winters when no inspections were done.

Winter	Observed individuals	TRIM index	Estimated individuals	SE
2004/2005	5	1	5	5
2005/2006	-	1.2192	6	3
2006/2007	-	1.4987	8	3
2007/2008	-	1.8424	10	4
2008/2009	-	2.2648	12	4
2009/2010	-	2.7841	15	4
2010/2011	-	3.4225	18	5
2011/2012	24	4.3923	24	10
2012/2013	-	5.2987	27	6
2013/2014	36	6.9713	36	12
2014/2015	-	7.6223	41	6
2015/2016	-	9.6077	51	6
2016/2017	63	11.9867	63	16
2017/2018	65	13.0798	69	18
2018/2019	92	17.5044	92	20
2019/2020	101	20.2935	107	22
2020/2021	148	29.4829	155	25

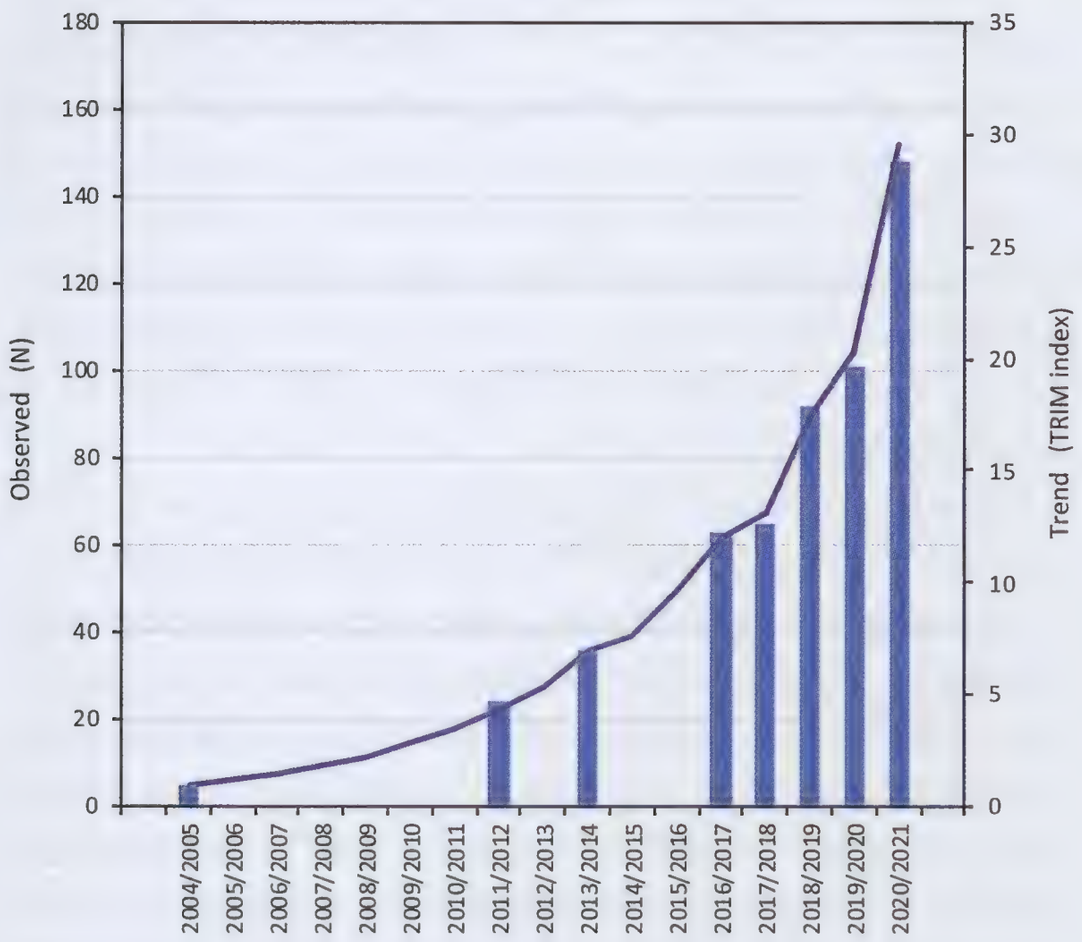

Fig. 2. Variation of wintering *Rhinolophus ferrumequinum* bats in the period 2004/2005 - 2020/2021.

Summer-autumn census
Data on the activity of bat species, or bat acoustic groups, in the four different habitats surrounding the cave area are reported in Table 2. The most utilized habitat was the agricultural mosaic with light, which showed a 2-3-fold activity level respect to the other habitats. These high activity levels were mainly due to the most ubiquitous species of the genus *Pipistrellus* and of the acoustic group *Eptesicus/Nyctalus/Vespertilio*.
The habitats utilized by the higher number of species were the woods and the cave entrances. The most active species in all four habitat categories was *Pipistrellus pipistrellus*, while the acoustic group *kuhlii/nathusii* was particularly active in the agricultural mosaic with light, as well as *Nyctalus leisleri*.
Several species where rarely observed (Table 2), except for the high activity of *Rhinolophus ferrumequinum* recorded in the area surrounding the cave entrances.

Incidental observations
A checklist of all species observed in the Fenera cave area is reported in Table 3. The list includes the incidental observations reported below:
- *Tadarida teniotis*: recorded with a bat-detector at the entrance of Ciota Ciara cave on 6 October 2012;
- *Rhinolophus ferrumequinum*: a single individual roosting in a small building at Colma (summer 2018);
- *Pipistrellus pipistrellus*: 1 ind. recorded with a bat-detector at the entrance of Ciota Ciara cave (summer 2018); 1 ind. found dead at Colma (summer 2018); 2 ind. roosting in the roof of a house at Maretti Valduggia (summer 2020);
- *Plecotus austriacus*: 1 ind. found dead at Zuccaro Valduggia on 17 June 2021;
- *Plecotus auritus*: 2 ind. captured by mist net at the entrance of Ciota Ciara cave on 6 October 2012.

DISCUSSION

Our study reports the presence of 18 species of bats found wintering or flying in the area surrounding cave entrances in a karstic area with several caves in NW Italy. In the winter period, according to visual inspections of caves, hibernating bats were almost exclusively *Rhinolophus ferrumequinum*. This species is scored as Near Threatened in the European Mammal Assessment (Temple & Terry, 2007). Situations of local extinction of the species have been reported in parts of England, Holland, Israel. Negative demographic trends were recorded in Austria, Belgium, Germany, Bulgaria, France, and Switzerland, followed only recently by a positive trend (Van der Meij *et al.*, 2015). In Great Britain, numerical decreases have been documented in the early 60s and 80s, while current populations seem stable. In Italy the species was probably abundant in the last century (Gulino & Dal Piaz, 1939), but surveys

Table 2. Activity of bat species or bat acoustic groups in four environments surrounding the cave entrances in Fenera's area. Activity is reported as mean number of bat passes per hour.

Species/Acoustic groups	**Woods**	**Cave entrances**	**Dark agricultural mosaic**	**Agricultural mosaic with light**
Barbastella barbastellus	0.03	0	0	0.03
Eptesicus serotinus	0.38	0.12	0.47	5.32
Eptesicus/Nyctalus/Vespertilio	0.45	0.10	0.21	17.97
Hypsugo savii	1.13	2.90	0.44	0.35
Myotis crypticus	0.03	0.38	0.02	0
Myotis daubentonii	0.10	0	0	0
Myotis emarginatus	0	0.18	0	0
Myotis HF	0.86	1.26	0.54	0.85
Myotis LF *myotis/blythii*	0.04	0.03	0.36	0.65
Nyctalus leisleri	0.05	0.03	3.44	23.82
Nyctalus noctula	0	0.05	0	0
Pipistrellus kuhlii	1.85	0.86	1.38	2.88
Pipistrellus kuhlii/nathusii	6.38	2.90	5.56	50.94
Pipistrellus pipistrellus	60.55	35.43	38.12	51.09
Pipistrellus pygmaeus	0.15	0.49	0	0
Plecotus sp.	0.01	0.02	0.48	6.38
Rhinolophus ferrumequinum	0.01	17.48	0.03	0
Tadarida teniotis	0	0	0.03	0
TOTAL BAT ACTIVITY (passes/hour)	**72.0**	**62.2**	**51.1**	**160.3**
Sampling effort (hours)	**79.5**	**115.5**	**66.5**	**34.0**

carried out recently show a notable rarefaction compared to the past (Agnelli *et al.*, 2004). The population is in decline due to the loss of foraging habitats, due to the intensification of agriculture and the use of pesticides, as well as to the reduction of adequate refuge sites. Large colonies are very rare (usually few individuals per colony, rarely more than 100 individuals). Our data highlight the importance of the Fenera caves as one of the most important wintering areas in NW Italy for this species. The large numerical increase that occurred during the last decade, as well as the high number of individuals counted in the last five years, are probably related both to the recent trend observed in NW Italy (Toffoli & Calvini, 2021) and to the conservation actions which have been put in place since the 1998, with the assembly of closed metal gates that prevent access to unauthorized tourists but allow the entry and exit of bats.

Our study highlights the interest of the Fenera as a foraging area utilized by *Rhinolophus ferrumequinum* during the summer and autumn seasons too. In NW Italy, during the 90s, observations of reproductive sites utilized in spring or summer were completely lacking (Sindaco *et al.*, 1992). To avoid possible disturbance of maternity roosts, we did not explore the caves in the summer period, but the presence of the species with high levels of activity is a good indication of reproduction in the area, considering that females usually have a much reduced home range during the lactating period (Jeon *et al.*, 2018). Alongside, there may have been a substantial contribution to the high activity rate of the area due to the presence of commuting males (Downs *et al.*, 2016) who possibly had daytime rest areas nearby. The presence of woods is also important for *Rhinolophus ferrumequinum*, the preferred foraging habitats of which are broad-leaved woodland interspersed with open spaces (Duvergé & Jones, 1994; Ransome & Hutson, 2000; Flanders & Jones, 2009).

Our study provides the first data of foraging activity in a NW Italy karstic area. The most utilized habitat was the agricultural mosaic with light, which showed a high activity level mainly due to the most ubiquitous species of the genus *Pipistrellus* and of the acoustic group *Eptesicus/Nyctalus/Vespertilio*. Besides, the habitats utilized by the higher number of species were the woods and the cave entrances. However, we underline that a fine comparison of the number of species in the different habitats would have required a much more extensive sampling, with the calculation of accumulation curves (Moreno & Halffter,

Table 3. Checklist of bats species observed in the caves of Fenera.
*: data reported in Pascutto & Balestrieri (2001) for the period 1993-1999, with supplementation from Lana *et al.* (2021) and the authors up to 2021.

Sites	*Tadarida teniotis*	*Rhinolophus ferrumequinum*	*Rhinolophus hipposideros*	*Barbastella barbastellus*	*Eptesicus serotinus*	*Hypsugo savii*	*M. alcathoe/brandtii/mystacinus*	*Myotis daubentonii*	*Myotis emarginatus*	*Myotis myotis/blythii*	*Myotis crypticus*	*Nyctalus leisleri*	*Nyctalus noctula*	*Pipistrellus kuhlii*	*Pipistrellus pipistrellus*	*Pipistrellus pygmaeus*	*Plecotus auritus*	*Plecotus austriacus*
Years 1993-1999 (2021)*																		
Bondaccia Cave		x	*							*							*	
Ciutarun Cave		x																
Ciota Ciara Cave		x	*															
Arenarie Cave		x																
Small caves		x	x							x								
Small building																		*
Years 2004-2020 (winter)																		
Bondaccia Cave		x					x			x								
Ciutarun Cave		x																
Ciota Ciara Cave		x									x							
Arenarie Cave		x																
Year 2020 (acoustic)																		
Cave entrances		x			x	x			x	x	x	x	x	x	x	x		
Woods		x		x	x	x		x		x	x	x		x	x	x		
Agricultural mosaic with light				x	x	x				x		x		x	x			
Dark agricultural mosaic	x	x			x	x				x	x	x		x	x			

2001; Skalak *et al.*, 2012). These habitats were utilized by some rare species, i.e. *Barbastella barbastellus* (Toffoli & Cucco, 2020) and all species of the genus *Myotis*. Our results are in line with the observations of Zukal & Řehák (2006) in the Moravian karst, with the exception of the high bat activity noted over Moravian ponds, a habitat that was not present in the Fenera area. The importance of karstic areas outside of the hibernating period has been underlined in several tropical zones (Struebig *et al.*, 2009; Racey & Furey, 2014), but has been little studied in temperate areas. Our results underline the importance of protecting the cave underground system as well as the habitats surrounding cave entrance for an effective conservation of bat biodiversity.

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Female reproductive characteristics of the Balkan sand lizard *Lacerta agilis bosnica* (Schreiber, 1912)

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Abstract: The sand lizard (*Lacerta agilis*), which occupies a large part of temperate Eurasia and includes several morphologically and genetically distinct lineages, is a model species for life-history studies. Yet, for major parts of the species range, basic data on female reproductive traits are lacking. Here we present the first data on female reproductive traits of *Lacerta agilis bosnica*, a poorly studied lineage inhabiting montane areas of the Balkan Peninsula. Ten females caught in mid-June 2017 on Mt. Maljen (950 m a.s.l.) in western Serbia were monitored and examined in the lab, as well as their eggs and hatchlings. We additionally examined the state and number of oocytes in 31 females from scientific collections. Mean clutch size is quite high (8.0 ± 0.4 eggs) in relation to small mean snout-vent length of gravid females (74 ± 1 mm), mean relative clutch mass is relatively low (0.37 ± 0.02), and egg incubation period (51 ± 1 days at 24-26 °C) is rather long for *L. agilis*. While mean values of the above traits are within the variation range found across conspecific populations studied thus far, mean values for egg size (mass, 0.42 ± 0.02 g; length, 11.8 ± 0.2 mm; width, 7.7 ± 0.1 mm) and hatchling size (mass, 0.47 ± 0.03 g; SVL, 25.0 ± 0.5 mm; tail length, 30.4 ± 1.6 mm) are clearly smaller than in all previously studied populations of this species.

Keywords: Clutch size - egg size - hatchling size - life-history - lacertid lizard - female reproductive output - Balkan Peninsula.

INTRODUCTION

The quantity and quality of the offspring a female produces determine her evolutionary fitness and ultimately the viability of the population. Therefore, offspring body size, offspring number, and other characteristics of female reproductive output are primary targets of evolutionary and ecological studies (Roff, 2002). Lizards exhibit a pronounced variation in reproductive traits within and among species, and they belong to model groups for studying the evolution of life-histories (Vitt & Pianka, 1994; Bauwens & Díaz-Uriarte, 1997; Shine, 2005).

The sand lizard (*Lacerta agilis* Linnaeus, 1758), which occupies a large part of temperate Eurasia and includes several morphologically (Bischoff, 1984, 1988) and genetically (Kalyabina-Hauf & Ananjeva, 2004; Joger *et al*., 2007; Andres *et al.,* 2014) distinct lineages (subspecies), exhibits pronounced variation in reproductive traits among individual females and over years within populations (Olsson & Shine, 1996, 1997a, b; Olsson & Madsen, 2001; Olsson *et al*., 2018; Shine *et al*., 2018), as well as between geographically distinct subspecies (Roitberg *et al*., 2015). Yet, the available reproductive data for *L. agilis* are still far from appropriate covering the major geographic areas and taxonomical units, especially for relative clutch mass and offspring size (Roitberg *et al*., 2015). For instance, for a large portion of the species range from the Pyrenees to western parts of Russia inhabited by *L. a. agilis* (sensu lato), *L. a. bosnica* (Schreiber, 1912) and *L. a. chersonensis* (Andrzejowski, 1832) (see fig. 1 in Roitberg *et al*., 2015 for geographic ranges of the widely recognized subspecies), data on these traits are only available for South Sweden (Olsson & Shine, 1997a; Olsson & Madsen, 2001) and Middle Europe (Rykena, 1988a), the latter region being represented by a small compound sample. Specifically, for *L. a. bosnica*, a distinct lineage restricted to higher elevations in montane areas of the Balkan Peninsula (Bischoff, 1984,

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1988; Andres *et al.,* 2014), any reproductive data are lacking. The reproductive life-history of this potentially endangered form (e.g. Sterijovski & Arsovski, 2019), which occupies the southern limits of the species range (Korsós & Bischoff, 1997), is important from a nature protection perspective. Furthermore, data on this lineage could help to disentangle the effects of ancestry and those of environmental and spatial factors in range-wide comparative studies on *L. agilis* (Roitberg, 2007; Roitberg *et al*., 2015). This is because *L. a. bosnica* is geographically adjacent to the western subspecies group (*L. a. agilis* sensu lato and *L. a. chersonensis*), while being phylogenetically closer to the eastern subspecies group (*L. a. exigua* Eichwald, 1831, sensu lato) (Kalyabina-Hauf & Ananjeva, 2004; Joger *et al*., 2007; Andres *et al*., 2014).

Here we present the first data on female reproductive traits of *L. a. bosnica* obtained via monitoring field-caught females and their eggs in the lab and via inspecting the reproductive state of preserved specimens from scientific collections. The main site was Mt. Maljen (44°06'N, 19°59'E; ca. 950 m a. s. l.) located on the Divčibare plateau in western Serbia (Fig. 1). This area has a humid temperate continental climate influenced by the proximity of higher mountains (Popović & Obratov-Petković, 2005). Sand lizards inhabit meadows (*Poa molinieri* - *Plantaginetum holostei* association) surrounded by pine forest (*Pinetum nigrae – P. sylvestris* association).

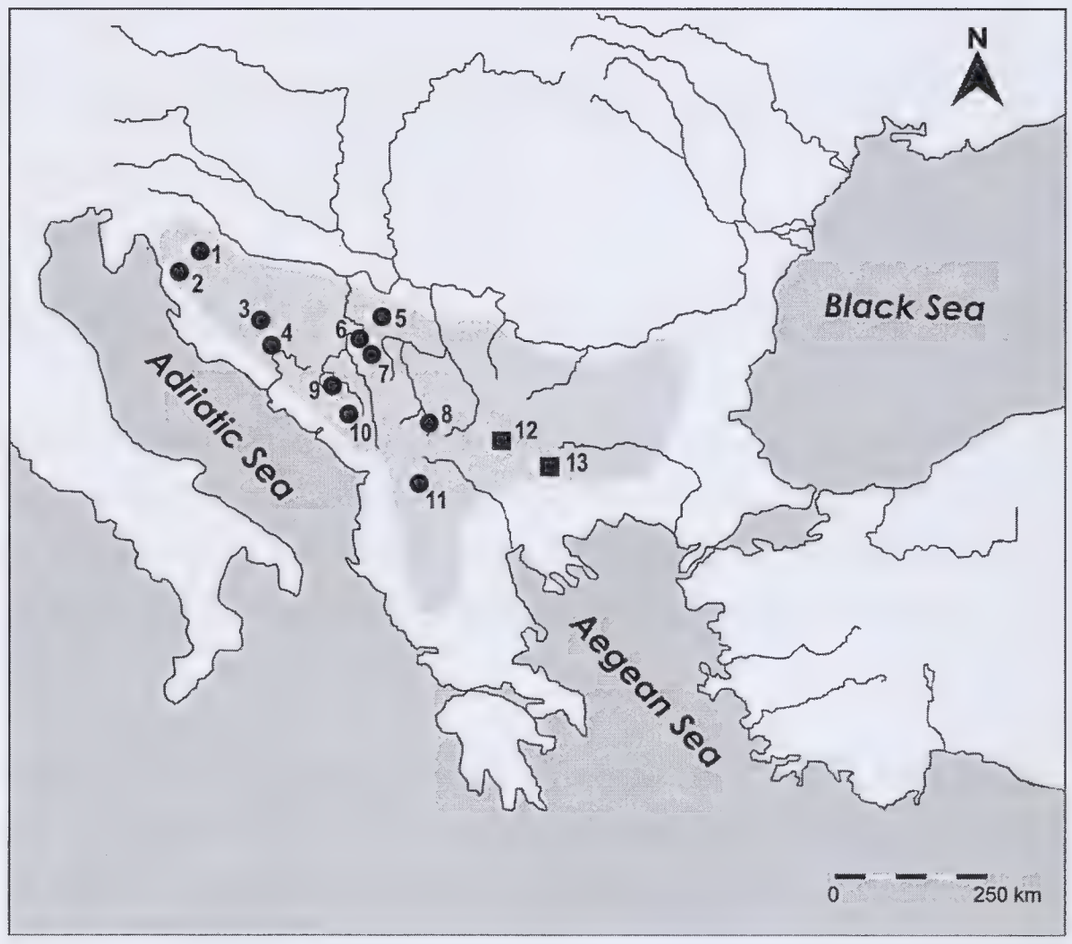

Fig. 1. Geographic range of *Lacerta agilis bosnica* (after Bischoff, 1988) and our study samples belonging to Dinaric (circles) and Balkan-Rhodope (squares) mountain systems. Numbers correspond to those in Appendix.

MATERIAL AND METHODS

Our data consist of two parts. A full set of female reproductive traits, including clutch mass and several aspects of egg and hatchling size, was studied in individuals coming from the West Serbian site Mt. Maljen (see above). Ten females at advanced stages of pregnancy caught between 8-15 June 2017 were transported to the Institute for Biological Research "Siniša Stanković" in Belgrade and housed individually in terraria (50 × 30 × 30 cm) with a substrate of sand, with pieces of bark, moss and leaf litter serving as shelters. The terraria were exposed to natural and additional artificial light that created a thermal gradient of ca. 18-40 °C from 7 a.m. to 7 p.m. Food (mealworms and maggots) and water were provided *ad libitum*. The females were inspected daily. Following oviposition, they were measured for snout-vent length (SVL) and weighed. Within 12 hours after oviposition, eggs were dug up, weighed, and measured for maximum length and width.

The eggs were marked and placed in plastic boxes filled with moistened vermiculite (volume ratio of vermiculite to water was 10:1). The eggs were checked daily to verify their viability. The moisture of the substrate was also checked daily and, if necessary, distilled water was added to compensate for water absorbed by the eggs and for losses due to evaporation. Room temperature was kept within 24-26 °C during the incubation period. Hatchlings were weighed and measured for SVL and total length within 12 hours after their emergence. The incubation time was defined as the number of days elapsed from egg-laying to hatchling emergence.

The second part of our data comes from recording the reproductive status and the number of oocytes in 31 gravid females of *L. a. bosnica* collected in different localities and deposited in zoological collections (see Fig. 1 and Appendix). By relating the oocyte stages (enlarged vitellogenic follicles, oviductal eggs) and internal marks of recent oviposition (widened oviducts and *corpora lutea*) to the capture dates we could roughly estimate the timing of consecutive events of the female reproductive cycle, i.e. the reproductive phenology. Specifically, a simultaneous occurrence of vitellogenic follicles and oviductal eggs or *corpora lutea* would argue for the occurrence of multiple clutches. For assessing reproductive phenology only specimens with precise collection dates were used. Considering that means of clutch size computed for different oocyte stages (enlarged follicles vs. oviductal eggs vs. laid eggs) did not differ significantly in *L. agilis* (Amat *et al*., 2000; Roitberg *et al*., 2015), counting enlarged follicles or oviductal eggs provided additional data on the clutch size - female size relationship. Linear measurements were taken with a digital caliper (0.01 mm precision), while mass was measured with an electronic balance (accuracy 0.001 g). Descriptive statistics (range, mean ± standard error, standard deviation) were calculated for original data. To avoid the problem of statistical non-independence of data collected from siblings, we used the mean value

for each clutch as the observation unit for egg and hatchling traits (e.g. Olsson & Shine, 1997a; Olsson & Madsen, 2001; Li *et al*., 2013; Roitberg *et al*., 2015). However, considering each hatchling as an independent observation did not significantly bias the results (Sorci & Clobert, 1999; Roitberg *et al*., 2013, 2015). Hence, when comparing our data with those from other *L. agilis* populations (see Discussion) we considered studies derived with both approaches. The slope of the clutch size - female size relationship was estimated using the reduced major axis regression (see Roitberg *et al*., 2015 for details and references). For other statistical analyses, all variables were log-transformed to approach data normality and homogeneity of variances (Sokal & Rohlf, 1981). Specifically, using general linear models (GLMs), we tested whether clutch size, maternal SVL, and their relationship differ between the following samples: I, living females from Mt. Maljen; II, preserved females from other sites in the Dinaric mountain system; III, preserved females from the Balkan-Rhodope mountain system (see Fig. 1 for geographic affinities of the three samples). All computations were done in the Statistica 10.0 for Windows package (StatSoft, Tulsa, OK, USA).

RESULTS

Seasonal variation in the reproductive stage in autopsied females from zoological collections with precise collection dates and those monitored in laboratory conditions is summarized in Fig. 2. Females with enlarged vitellogenic follicles were recorded from the second half of April to the first half of May. Capture dates of females with oviductal eggs ranged from the second half of May to the end of June. Oviposition in laboratory conditions took place in the second half of June. None of the examined females exhibited a simultaneous presence of enlarged vitellogenic follicles and oviductal eggs or *corpora lutea*; no other evidence for iteroparity was found.

Neither mean clutch size, nor mean maternal SVL differed significantly among the three study samples (Mt. Maljen females, other Dinaric females, Balkan-Rhodope females): ANOVA: $F_{2,38} = 0.86$, $p = 0.43$ and $F_{2,38} = 0.56$, $p = 0.58$ for clutch size and maternal SVL, respectively. GLM with clutch size as the response variable and maternal SVL as the covariate also exhibited no significant effect of the sample identity both in a separate slope model (Sample, $F_{2,35} = 0.12$, $p = 0.89$; Sample × Maternal SVL, $F_{2,35} = 0.10$, $p = 0.91$; Maternal SVL, $F_{1,35} = 28.44$, $p < 0.001$) and in ANCOVA (Sample,

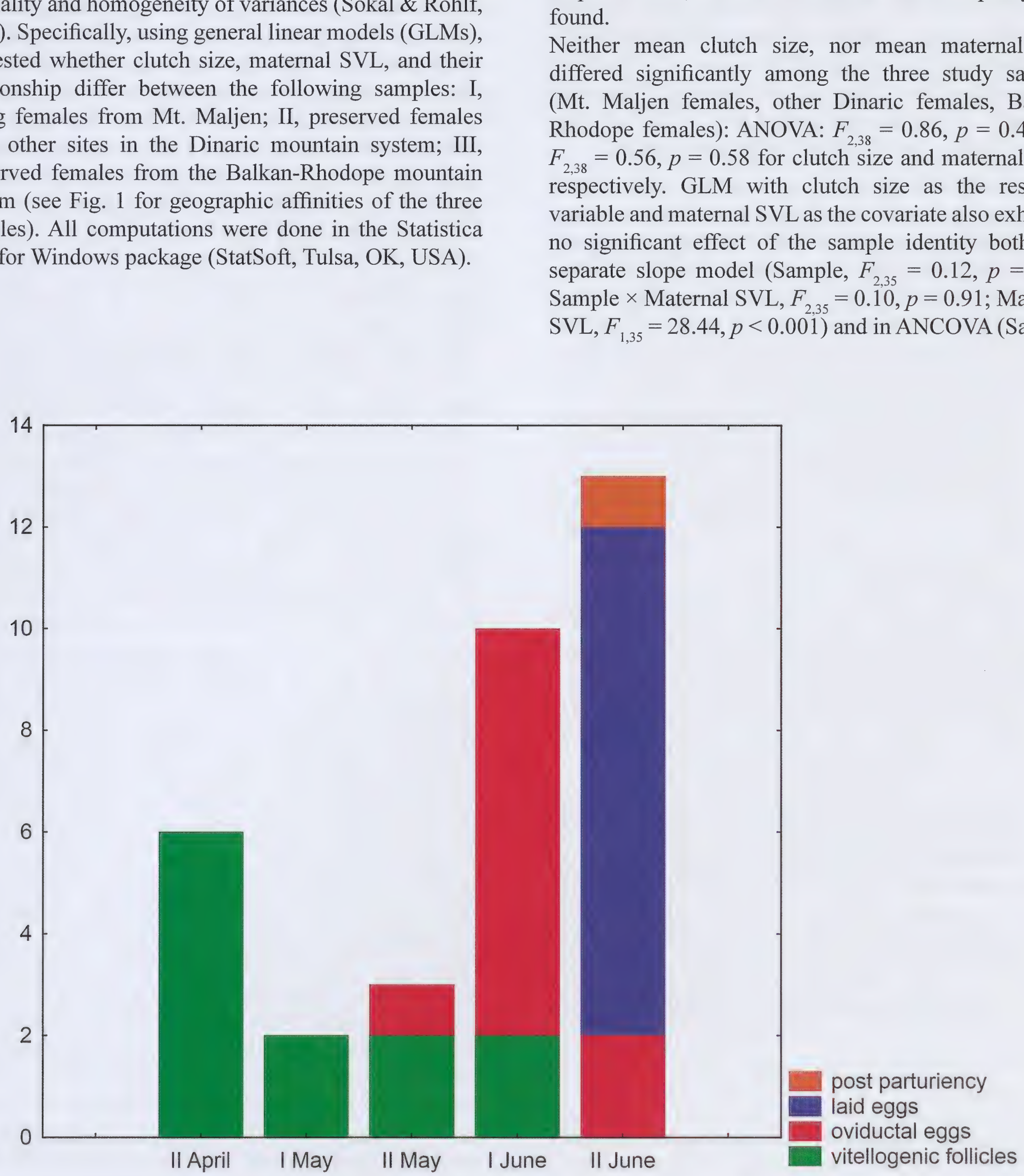

Fig. 2. Number of *L. a. bosnica* adult females in different reproductive stages during three months, presented for half-month periods.

$F_{2,37} = 0.76$, $p = 0.48$; Maternal SVL, $F_{1,37} = 48.45$, $p < 0.001$). Therefore, RMA regression slope of clutch size on maternal SVL and Pearson correlation coefficient (r) between the two traits were computed for the pooled sample: slope, 0.38 ± 0.04; correlation, 0.76 ± 0.10; $n = 41$. Fig. 3 visualizes the results presented above.

Table 1 describes the variation of 12 reproductive traits studied in ten living females from Mt. Maljen. While SVL of the post-oviposition females from Mt. Maljen is less variable than SVL of females which carry oviductal eggs or enlarged follicles and come from diverse localities (70-81 vs. 63-84 mm), the mean values of the two samples are very similar (75.2 vs. 74.2 mm). The clutch size of the Mt. Maljen females studied in the lab was similar to that in the sample from collections for both the ranges (5-12 vs. 4-12) and the means (7.8 vs. 8.0). Thus, as regards the clutch size and maternal SVL central tendencies, the ten females studied for a full set of traits are well representative for the whole study sample.

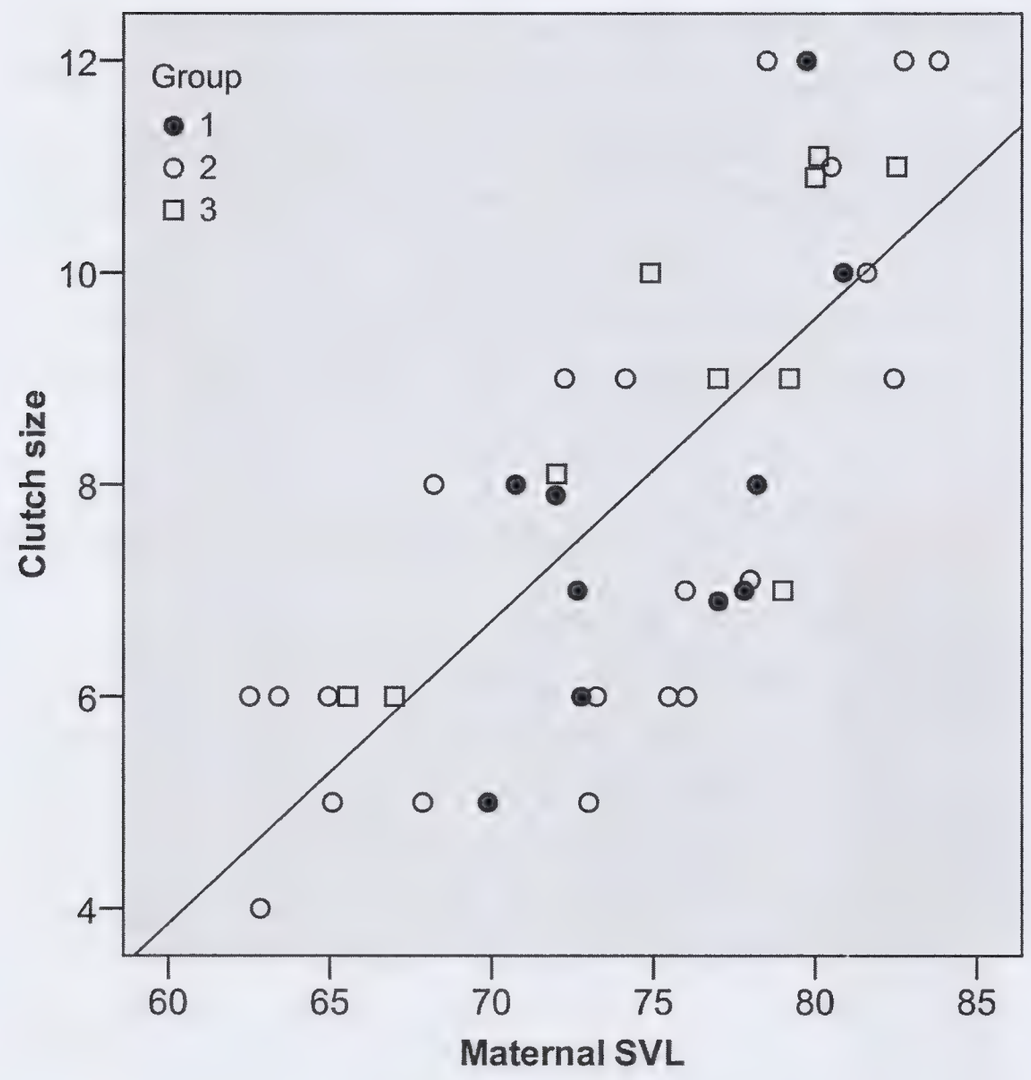

Fig. 3. Clutch size and maternal SVL for 41 studied females of *Lacerta agilis bosnica*. Regression line is shown for the pooled sample only, because no differences in the clutch size – maternal SVL relationship between the three groups were found (see text for details). Groups: 1, living females from Mt. Maljen; 2, preserved females from the Dinaric mountain system; 3, preserved females from the Balkan-Rhodope mountain system (see Fig. 1 for geographic affinities of the three samples).

DISCUSSION

Data on reproducing females collected at different dates (Fig. 2) show that each oocyte stage (enlarged follicles, oviductal eggs or *corpora lutea*) is associated with a moderate range of capture dates (five weeks or less). This pattern, and particularly the lack of simultaneous presence of different oocyte stages in individual females, argue that female *L. a. bosnica* apparently lay a single clutch annually, oviposition likely occurring from early June to early July.

Mean clutch size is quite high in relation to small mean SVL of gravid females (Kidov *et al.*, 2012, 2014; Kidov & Kovrina, 2015; Kidov & Matushkina, 2017; Roitberg *et al.*, 2015 and references therein), mean RCM is relatively low (Roitberg *et al.*, 2015 and references therein), and egg incubation period is rather long for *L. agilis* (Li *et al.*, 2013; Rykena, 1988b and references therein; Warnecke, 2000; Sobocinski & Maślak, unpubl. data).

While mean values of the above traits are within the variation range found across conspecific populations studied thus far, mean values for egg and hatchling size are smaller than in all previously studied populations of this species. So in *L. a. agilis* sensu lato, the lineage exhibiting the smallest egg and offspring size (Roitberg *et al.*, 2015), mean egg mass ranged from 0.56 to 0.60 g (Amat *et al.*, 2000; Rykena, 1988a; Olsson & Madsen, 2001), mean hatchling mass from 0.57 to 0.59 g (Rykena, 1988a; Olsson & Shine, 1997b; Olsson & Madsen, 2001), mean hatchling SVL from 28.3 to 30.7 mm (Rykena, 1988a; Langford, 1985; Barus & Oliva, 1992). Bosch & Bout (1998) reported a mean hatchling SVL of 24.6 mm which is slightly lower than in our study. However, this value might well be wrong, since the corresponding means for egg mass, hatchling mass, and tail length (respectively, 0.66 g, 0.70 g, 41.5 mm; Bosch & Bout, 1998) are much larger than in our *L. a. bosnica* sample. Recently Georgieva & Vergilov (2020) reported a mean hatchling mass of 0.49 g (*L. a. chersonensis*, Western Bulgaria) which is only slightly larger than in our study. Yet, their report is based on a single clutch; moreover, the mean SVL of this clutch (30.3 mm) was markedly higher than all clutch means of the Mt. Maljen sample (Table 1). A deviation in any particular trait, especially linear measurements, can be caused by inter-observer bias (Roitberg *et al.*, 2011 and references therein) and other systematic differences which might exist among studies (e.g. they might differ in mean time between oviposition and measuring eggs). However, small egg and hatchling size in our study sample can hardly be solely explained by such biases considering that six different traits show lower mean (and minimum) values than those in all previously studied populations, which range from the Pyrenees to Siberia and China and represent three distinct lineages (*L. a. agilis* sensu lato, *L. a. exigua* sensu lato, and *L. a. boemica* Suchow, 1929). Taking into account that our egg and hatchling size data come from ten females collected during eight days of a single year within a small area of 100 ha, statistical distributions of the studied traits (except clutch size and SVL of gravid females which we obtained from a larger and more diversified sample) might have been impacted by a local or temporal fluctuation. Yet, the small offspring size in our study

Table 1: Variation of female reproductive traits in *Lacerta agilis bosnica* from Mt. Maljen, Serbia.

Trait	N	range	mean ± SE	SD
Female SVL (mm)	10	69.88 – 80.87	75.16 ± 1.26	3.87
Clutch size	10	5 – 12	7.8 ± 0.63	1.99
Post-oviposition female body mass (PM, g)	10	6.990 – 12.393	8.778 ± 0.523	1.655
Clutch mass (CM, g)	10	2.003 – 5.591	3.279 ± 0.321	1.014
Relative clutch mass (RCM = CM/PM)	10	0.287 – 0.451	0.369 ± 0.019	0.059
Egg mass (g)	10	0.354 – 0.499	0.418 ± 0.015	0.047
Egg length (mm)	10	10.60 – 13.10	11.75 ± 0.22	0.70
Egg width (mm)	10	7.19 – 8.34	7.67 ± 0.12	0.37
Hatchling SVL (mm)	9	22.23 – 27.13	25.01 ± 0.48	1.44
Hatchling tail length (mm)	9	20.03 – 36.34	30.43 ± 1.59	4.80
Hatchling mass (g)	9	0.298 – 0.608	0.473 ± 0.029	0.086
Incubation duration (days)	9	48 – 53	50.81 ± 0.51	1.53
Duration in captivity prior to oviposition (days)	10	7-16	11.00 ± 0.94	2.98

sample is unlikely to be solely a fluctuation of this kind. In a *L. a. agilis* population (Asketunnan, South Sweden), which was studied over 20 years, mean hatchling mass was recorded in 561 clutches of 353 individual females (Ljungström *et al*., 2016), thus providing exceptionally reliable estimates of the variation range. The minimum value of the mean hatchling mass in this huge sample was 0.42 g (Ljungström *et al*., 2016), which is much higher than in our study (0.30 g – Table 1). Furthermore, neither the sampling year (2017) nor the previous one appeared to exhibit markedly deviating weather conditions in the Mt. Maljen study site. The time in captivity from capture to oviposition, a factor known to negatively affect egg and offspring size in squamates (King, 1993; Recknagel & Elmer, 2019; Roitberg & Eplanova, unpubl. data) was quite low (Table 1), and thus hardly influential, in our study.

Apart from low egg and hatchling size, the studied *L. a. bosnica* shows an unusual trait combination: higher clutch size relative to female size, as well as smaller egg and offspring size resemble it to the western lineage *L. a. agilis*. In contrast, lower relative clutch mass and longer egg incubation period found in the Mt. Maljen females are proper to the eastern forms *L. a. exigua* and *L. a. boemica* (Roitberg *et al*., 2015 and references therein). To conclude, the presented data argue for a distinct reproductive strategy in *L. a. bosnica*, but further life-history studies, preferably involving multiple localities with contrasting environments, will show to what extent the revealed reproductive pattern reflects some stable characteristics of a distinct life-history strategy in this interesting but understudied lineage.

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APPENDIX 1

Localities of population samples, including geographical coordinates, altitude, sample size and zoological collection. IBISS – Institute for Biological Research, Belgrade, Serbia; MTD - Senckenberg Natural History Collections Dresden, Germany; ZFMK - Zoological Research Museum A. Koenig Bonn, Germany; ZSM - Zoological State Collections Munich, Germany. 1. Croatia, Mt. Mala Kapela, Plitvička lakes (44.8696°N, 15.6280°E, 675 m, 2, IBISS); 2. Croatia, Mt. Velebit hinterland, Bužim village (44.5755°N, 15.2524°E, 562 m, 1, IBISS); 3. Bosnia & Herzegovina, Mt. Cincar, Gornja Malovan village (43.9277°N, 17.2003°E, 1140 m, 1, IBISS); 4. Bosnia & Herzegovina, Mt. Čvrsnica, Lake Blidinje (43.6179°N, 17.4702°, 1205 m, 1, IBISS); 5. Serbia, Mt. Maljen, Divčibare plateau (44.1085°N, 19.9889°E, 950 m, 1, IBISS); 6. Serbia, Mt. Tara, Golubovac and Karaića bare (43.8884°N, 19.4491°E, 1245m, 3, IBISS); 7. Serbia, Mt. Zlatibor (43.7175°N, 19.7062°E, 1007 m, 7, IBISS); 8. Serbia, Mt. Kopaonik, Trepča (42.9423°N, 20.9221°E, 840 m, 1, IBISS); 9. Montenegro, Mt. Durmitor (43.1564°N, 19.1136°E, 1417 m, 1, IBISS); 10. Montenegro, Mt. Prekornica, Srednja Ponikvica (42.6739°N, 19.2671°E, 1400 m, 1, IBISS); 11. North Macedonia, Mt. Bistra, Galičnik (41.6269°N, 20.6854°E, 1600 m, 1, IBISS) and Mt. Dešat, Lake Lokuvsko (41.6352° N, 20.5604°E, 1582 m, 1, IBISS); 12. Serbia, Mt. Dukat, Karamanica (42.3537°N, 22.3155°E, 1417 m, 2, IBISS); 13. Bulgaria, Mt. Pirin, (Pirin s.l. 5, ZFMK; Banderija, Khomutivskyi Step, 41.7779°N, 23.4370°E, 1650 m, 1, ZSM; Begovitza Chalet, 41.6739°N, 23.4274°E, 2000-2200 m, 2, MTD).

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The species described by René-Édouard Claparède. Part 1: Animalia

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Abstract: René-Edouard Claparède, an often overlooked Genevan zoologist, described nearly 200 species of animal in his short career. These are listed with the currently valid combinations.

Keywords: Geneva - Annelida - marine invertebrates - Naples.

INTRODUCTION

The year 2022 marks the 150th anniversary of the Natural History Museum of Geneva (MHNG) as an independent institution. It seems fitting to mark this by filling one of the lacunae left in the story of the Museum published for the bicentenary of the inauguration of the Musée Académique in 1820 (Ayer *et al.*, 2020); the contribution of René-Édouard Claparède (1832-1871, known to his contemporaries as Édouard) to taxonomy (Fig. 1).

Claparède studied in Geneva (1850-1852), where he was greatly influenced by François-Jules Pictet (1809-1872), and Berlin (1853-1857) where he studied medicine and worked in the laboratory of Johannes Müller (1801-1858). He returned to Geneva with a medical doctorate and became professor of zoology, first as assistant to Pictet and then, from 1863, as full professor. As professor he was a member of the Commission d'Administration responsible for the Musée Académique (forerunner of the MHNG) and its collections. He published on the histology, embryology, physiology and systematics of invertebrates. His early work, under the influence of Müller and Christian Ehrenberg (1796-1876), concentrated on what were then known as the Infusoria (currently placed in the Ciliophora), but after a trip to Scotland with William Carpenter (1813-1885) his focus changed to marine annelids (Saussure, 1873).

Plagued by ill health from his youth, Claparède died in Sienna while returning from spending the winter in Naples for health reasons. The MHNG collections contain 18 boxes of histological slide preparations of Polychaeta made by Claparède (remounted by Hermann Fol in 1872) but none of the type specimens of the species he described has been traced and they are generally considered to have been lost. Many of his contributions were considered import in their day, but increasingly sophisticated techniques, his early death and confusion with his nephew Édouard Claparède (1873-1940), neurologist, psychologist and educator, have serve to limit his fame more than he deserves.

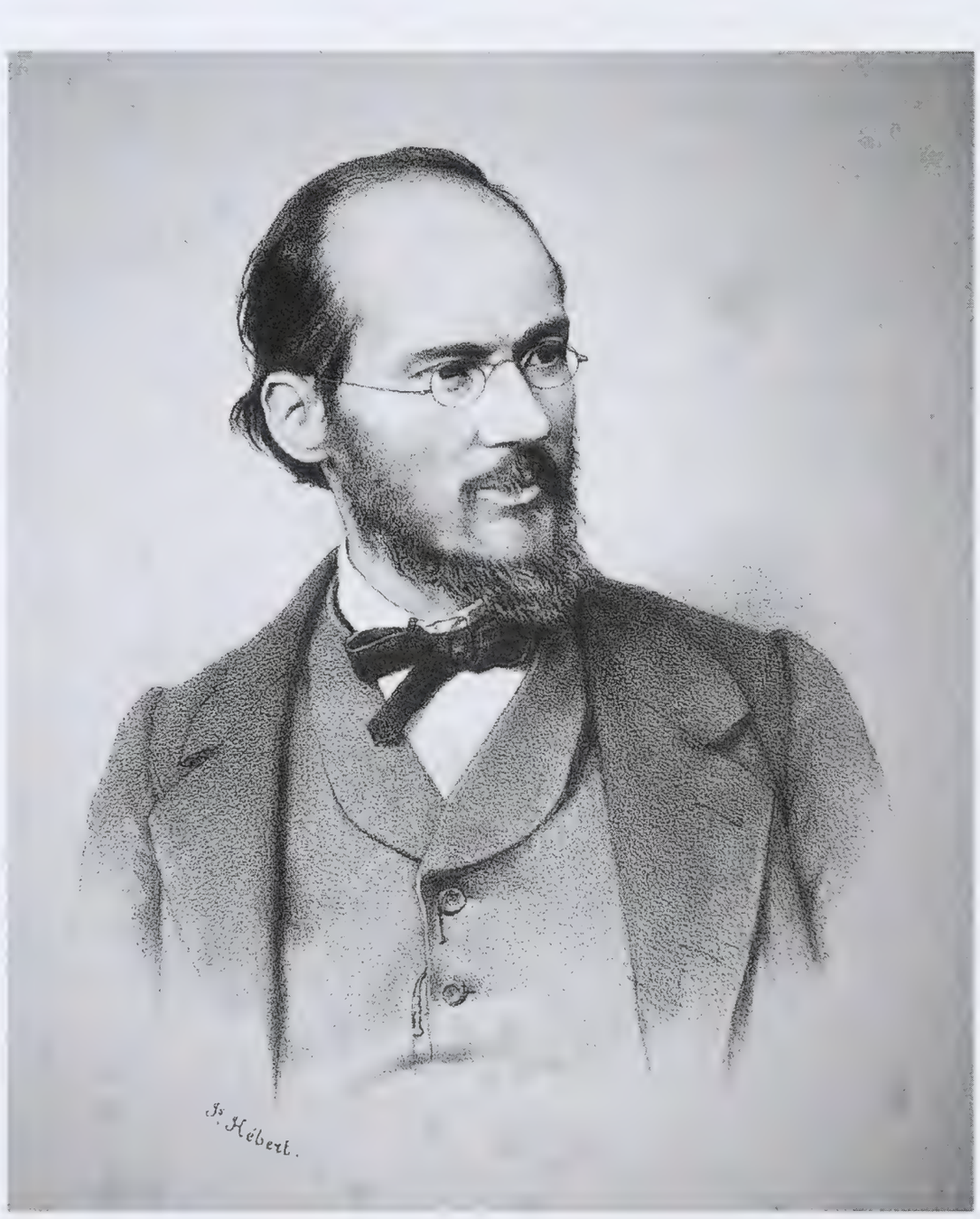

Fig. 1. Portrait of René-Édouard Claparède, published in Saussure (1873). Public domain.

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ARRANGEMENT AND FORMAT

Claparède is the author of 48 genus level names and 197 species level names of organisms currently classified in the kingdom Animalia. These are listed here along with the currently valid combination. The groups are listed alphabetically by phylum, class and family with first the generic names and then the species names in alphabetic order. Nomenclature follows the WoRMS database (WoRMS editorial board, 2021) unless explicitly stated.

ANIMAL SPECIES DESCRIBED BY RENÉ-ÉDOUARD CLAPARÈDE

Phylum Annelida

Class Clitellata
Family Enchytraeidae

Pachydrilus Claparède, 1861: 75-76.
A junior synonym of *Lumbricillus* Örsted, 1844

crassus Claparède, 1861: 79-81, pl. 2 figs 6-9. [*Pachydrilus*]
Lumbricillus crassus (Claparède, 1861)

ebudensis Claparède, 1861: 85-86, pl. 1 fig. 8. [*Pachydrilus*]
Lumbricillus ebudensis (Claparède, 1861)

lacteus Claparède, 1861: 85. [*Pachydrilus*]
Lumbricillus lacteus (Claparède, 1861)

semifuscus Claparède, 1861: 76-79, pl. 2 figs 1-5. [*Pachydrilus*]
Claparedrilus semifuscus (Claparède, 1861)

verrucosus Claparède, 1861: 82-85, pl. 1 figs 1-6. [*Pachydrilus*]
A junior synonym of *Lumbricillus lineatus* (Müller, 1774)

Family Haplotaxidae

Nemodrilus Claparède, 1862: 275.
A junior synonym of *Haplotaxis* Hoffmeister, 1843

filiformis Claparède, 1862: 275-276. [*Nemodrilus*]
A junior synonym of *Haplotaxis gordoides* (Hartmann in Oken, 1819)

Family Lumbriculidae

Stylodrilus Claparède, 1862: 262-263.
Stylodrilus Claparède, 1862

Trichodrilus Claparède, 1862: 267.
Trichodrilus Claparède, 1862

allobrogum Claparède, 1862: 267-270. [*Trichodrilus*]
Trichodrilus allobrogum Claparède, 1862

heringianus Claparède, 1862: 263-266. [*Stylodrilus*]
Stylodrilus heringianus Claparède, 1862

Family Naididae

*Heterochaet*a Claparède, 1863: 25.
A junior homonym replaced by *Baltidrilus* Timm, 2013

costata Claparède, 1863: 25, pl. 13 figs 16-19. [*Heterochaeta*]
Baltidrilus costata (Claparède, 1863)

Family Tubificidae

Limnodrilus Claparède, 1862: 243.
Limnodrilus Claparède, 1862

Pachydermon Claparède, 1861: 156.
Pachydermon Claparède, 1861

acuminatum Claparède, 1861: 156-7, pl. 4 figs 1-1a. [*Pachydermon*]
Pachydermon acuminatum Claparède, 1861

ater Claparède, 1862: 253-254. [*Clitellio*]
A junior synonym of *Tubificoides benedii* (d'Udekem, 1855)

bonneti Claparède, 1862: 230-243. [*Tubifex*]
A junior synonym of *Tubifex tubifex tubifex* (Müller, 1774)

elongatum Claparède, 1862: 254. [*Pachydermon*]
Pachydermon elongatum Claparède, 1862

hoffmeisteri Claparède, 1862: 248-252. [*Limnodrilus*]
Limnodrilus hoffmeisteri Claparède, 1862

papillosus Claparède, 1863: 25, pl. 13 figs 14-15. [*Tubifex*]
A junior synonym of *Tubificoides benedii* (d'Udekem, 1855)

udekemianus Claparède, 1862: 243-247. [*Limnodrilus*]
Limnodrilus udekemianus Claparède, 1862

Class Polychaeta
Family Ampharetidae

Branchiosabella Claparède, 1863: 34.
A junior synonym of *Ampharete* Malmgren, 1866

curvipalea Claparède, 1870a: 496, pl. 13 fig. 5. [*Amphicteis*]
A junior synonym of *Amphicteis gunneri* (Sars, 1835)

zostericola Claparède, 1863: 35, pl. 14 figs 12-17. [*Branchiosabella*]
A junior synonym of *Ampharete acutifrons* (Grube, 1860)

Family Arenicolidae

Clymenides Claparède, 1863: 30.
A junior synonym of *Arenicola* Lamarck, 1801

grubii Claparède, 1869: 36, pl. 19 fig. 2. [*Arenicola*]
A junior synonym of *Arenicolides branchialis* (Audouin & Milne Edwards, 1833)

sulphurea Claparède, 1863: 30, pl. 15 figs 24-27. [*Clymenides*]
A junior synonym of *Arenicola marina* (Linnaeus, 1758)

Family Capitellidae

benedeni Claparède, 1864: 514, pl. 4 fig. 9. [*Notomastus*]
A junior synonym of *Notomastus latericeus* Sars, 1851

costana Claparède, 1868: 15, pl. 27 fig. 2. [*Capitella*]
A junior synonym of *Heteromastus filiformis* (Claparède, 1864)

filiformis Claparède, 1864: 509, pl. 4 fig. 10. [*Capitella*]
Heteromastus filiformis (Claparède, 1864)

lineatus Claparède, 1869: 18, pl. 17 fig. 4. [*Notomastus*]
Notomastus lineatus Claparède, 1869

major Claparède, 1868: 16, pl. 17 fig. 3. [*Capitella*]
A junior synonym of *Notomastus profundus* (Eisig, 1887)

sarsii Claparède, 1864: 511, pl. 4 fig. 8, pl. 8 fig. 7. [*Notomastus*]
A junior synonym of *Notomastus lineatus* Claparède, 1869

Family Chaetopteridae

Ranzania Claparède, 1870a: 489.
A junior homonym replaced by *Mesochaetopterus* Potts, 1914

costarum Claparède, 1869: 80, pl. 20 fig. 1. [*Telepsavus*]
Spiochaetopterus costarum (Claparède, 1869)

fallax Claparède, 1869: 90, pl. 21 fig. 2. [*Phyllochaetopterus*]
A junior synonym of *Phyllochaetopterus socialis* Claparède, 1869

major Claparède, 1869: 92, pl. 19 fig. 1. [*Phyllochaetopterus*]
Phyllochaetopterus major Claparède, 1869

sagittaria Claparède, 1870a: 490, pl. 11 fig. 1. [*Ranzania*]
Mesochaetopterus sagittaria (Claparède, 1870)

socialis Claparède, 1869: 85, pl. 21 fig. 1. [*Phyllochaetopterus*]
Phyllochaetopterus socialis Claparède, 1869

Family Chrysopetalidae

Palmyra (*Palmyrides*) Claparède, 1864: 583.
A junior synonym of *Chrysopetalum* Ehlers, 1864

Palmyra (*Palmyropsis*) Claparède, 1864: 586.
A junior synonym of *Chrysopetalum* Ehlers, 1864

evelinae Claparède, 1864: 586, pl. 8 fig. 6. [*Palmyra* (*Palmyropsis*)]
A junior synonym of *Chrysopetalum debile* (Grube, 1855)

portusveneris Claparède, 1864: 583, pl. 8 fig. 5. [*Palmyra* (*Palmyrides*)]
A junior synonym of *Chrysopetalum debile* (Grube, 1855)

Family Cirratulidae

Ctenodrilus Claparède, 1863: 25.
Ctenodrilus Claparède, 1863

chrysoderma Claparède, 1868: 2, pl. 23 fig. 4. [*Cirratulus*]
Protocirrineris chrysoderma (Claparède, 1868)

pardalis Claparède, 1863: 25, pl. 15 figs 18-20. [*Ctenodrilus*]
A junior synonym of *Ctenodrilus serratus* (Schmidt, 1857)

Family Dorvilleidae

chiaji Claparède, 1868: 425, pl. 7 fig. 2. [*Staurocephalus*]
A junior synonym of *Schistomeringos rudolphi* (delle Chiaji, 1828)

Family Eunicidae

cingulata Claparède, 1868: 444, pl. 7 fig. 1. [*Eunice*]
A junior synonym of *Eunice purpurea* Grube, 1866

geniculatus Claparède, 1868: 459, pl. 6 fig. 6. [*Notocirrus*]
Arabella geniculata (Claparède, 1868)

mahagoni Claparède, 1864: 576, pl. 2 fig. 4. [*Lysidice*]
A junior synonym of *Lysidice ninetta* Audouin & Milne Edwards, 1833

margaritacea Claparède, 1868: 453, pl. 8 fig. 3. [*Lysidice*]
A junior synonym of *Lysidice ninetta* Audouin & Milne Edwards, 1833

multicirrata Claparède, 1863: 60, pl. 14 figs 23-26. [*Lysidice*]
Lysidice multicirrata Claparède, 1863 nomen dubium (juvenile *Marphysa*?)

schizobranchia Claparède, 1870a: 394, pl. 2 fig. 6. [*Eunice*]
Eunice schizobranchia Claparède, 1870

taenia Claparède, 1864: 580, pl. 4 fig. 11. [*Eunice*]
A junior synonym of *Palola sicilensis* (Grube, 1840)

Family Flabelligeridae

eruca Claparède, 1869: 105, pl. 25 fig. 2. [*Trophonia*]
Piromis eruca (Claparède, 1869)

Family Glyceridae

Rhynchobolus Claparède, 1868: 492.
A junior synonym of *Glycera* Lamarck, 1818

Family Hesionidae

Stephania Claparède, 1870a: 482. (Not listed in WoRMS)
A junior synonym of *Oxydromus* Grube, 1855

pallidus Claparède, 1864: 521, pl. 4 fig. 1. [*Oxydromus*]
Oxydromus pallidus Claparède, 1864

Family Lopadorrhynchidae

Hydrophanes Claparède, 1870a: 463-464.
A junior synonym of *Lopadorrhynchus* Grube, 1855

krohnii Claparède, 1870a: 464, pl. 11 fig. 2. [*Hydrophanes*]
Lopadorrhynchus krohnii (Claparède, 1870)

Family Lumbrineridae

edwardsii Claparède, 1863: 58, pl. 14 figs 16-22. [*Lumbriconereis*]
A junior synonym of *Lumbrineris latreilli* Audouin & Milne Edwards, 1833

impatiens Claparède, 1868: 455, pl. 9 fig. 2. [*Lumbriconereis*]
A junior synonym of *Scoletoma laurentiana* (Grube, 1863)

Family Maldanidae

collaris Claparède, 1869: 194, pl. 26 fig. 2. [*Praxilla*]
Euclymene collaris (Claparède, 1869)

constricta Claparède, 1869: 195, pl. 26 fig. 2. [*Axiothea*]
Axiothella constricta (Claparède, 1869)

cristagalli Claparède, 1869: 197, pl. 26 fig. 4. [*Maldane*]
A junior synonym of *Petaloproctus terricolus* Quatrefages, 1866

oerstedii Claparède, 1863: 28, plate13 figs 6-11. [*Clymene*]
Euclymene oerstedii (Claparède, 1863)

simplex Claparède, 1869: 192, pl. 27 fig. 7. [*Praxilla*]
Praxilella simplex (Claparède, 1869) nomen dubium

Family Nereididae

Cirroceros Claparède, 1863: 55.
Cirroceros Claparède, 1863 nomen dubium

Micronereis Claparède, 1863: 56.
Micronereis Claparède, 1863

antennata Claparède, 1863: 56, pl. 14 figs 8-12. [*Cirroceros*]
Cirroceros antennata Claparède, 1863 nomen dubium

ehlersiana Claparède, 1870a: 452, pl. 8 fig. 2. [*Nereis* (*Ceratonereis*)]
A junior synonym of *Ceratonereis* (*Composetia*) *hircinicola* (Eisig, 1870)

glauca Claparède, 1870a: 454, pl. 7 fig. 3. [*Nereis* (*Leptonereis*)]
Websterinereis glauca (Claparède, 1870)

guttula Claparède, 1868: 475, pl. 9 fig. 6, pl. 10 fig. 3. [*Nereis* (*Ceratonereis*)]
A junior synonym of *Ceratonereis* (*Composetia*) *costae* (Grube, 1840)

kinbergiana Claparède, 1870a: 453, pl. 8 fig. 3. [*Nereis* (*Ceratonereis*)]
A junior synonym of *Ceratonereis* (*Composetia*) *hircinicola* (Eisig, 1870)

macropus Claparède, 1870a: 444, pl. 8 fig. 1. [*Nereis* (*Lipephile*)]
Perinereis macropus (Claparède, 1870)

malmgreni Claparède, 1868: 483, pl. 11 fig. 1. [*Heteronereis*]
A junior synonym of *Platynereis dumerilii* (Audouin & Milne Edwards, 1833)

peritonealis Claparède, 1868: 467, pl. 9 fig. 5. [*Nereis*]
A junior synonym of *Platynereis dumerilii* (Audouin & Milne Edwards, 1833)

perivisceralis Claparède, 1868: 471, pl. 12 fig. 1. [*Nereis*]
Nereis perivisceralis Claparède, 1868

variegata Claparède, 1863: 56, pl. 11 figs 5-7. [*Micronereis*]
Micronereis variegata Claparède, 1863

Family Oenonidae

Drilonereis Claparède, 1870a: 399.
Drilonereis Claparède, 1870

filum Claparède, 1868: 454, pl. 9 fig. 1. [*Lumbriconereis*]
Drilonereis filum (Claparède, 1868)

Family Onuphidae

pancerii Claparède, 1868: 438, pl. 8 fig. 1. [*Onuphis*]
Onuphis pancerii Claparède, 1868

rigida Claparède, 1868: 441, pl. 8 fig. 2. [*Hyalinoecia*]
Aponuphis rigida (Claparède, 1868)

Family Opheliidae

pallidus Claparède, 1869: 34, pl. 31 fig.7. [*Polyophthalmus*]
A junior synonym of *Polyophthalmus pictus* (Dujardin, 1839)

Family Orbinidae

anserina Claparède, 1864: 504, pl. 4 fig. 6. [*Theodisca*]
A junior synonym of *Naineris laevigata* (Grube, 1855)

foetida Claparède, 1869: 45, pl. 20 fig. 2. [*Aricia*]
Phylo foetida (Claparède, 1869)

liriostoma Claparède, 1869: 50, pl. 24 fig. 2. [*Theodisca*]
A junior synonym of *Naineris laevigata* (Grube, 1855)

oerstedii Claparède, 1864: 502, pl. 4 fig. 7. [*Aricia*]
Protoaricia oerstedii (Claparède, 1864)

Family Pectinariidae

neapolitana Claparède, 1869: 113, pl. 28 fig. 1. [*Pectinaria*]
Lagis neapolitana (Claparède, 1869)

Family Phyllodocidae

Alciopina Claparède & Panceri, 1867: 5-8.
Alciopina Claparède & Panceri, 1867

Eulalia (*Pterocirrus*) Claparède, 1868: 558.
Pterocirrus Claparède, 1868

Vanadis Claparède, 1870a: 480.
Vanadis Claparède, 1870

armata Claparède, 1868: 550, pl. 17 fig. 5. [*Eteone*]
A junior synonym of *Mysta picta* (Quatrefages, 1866)

cephalotes Claparède, 1868: 548, pl. 17 fig. 3. [*Anaitis*]
Anaitis cephalotes Claparède, 1868 nomen dubium

corniculata Claparède, 1868: 546, pl. 17 fig. 1. [*Phyllodoce*]
A junior synonym of *Nereiphylla paretti* Blainville, 1828

formosa Claparède, 1870a: 480, pl. 10 fig. 3. [*Vanadis*]
Vanadis formosa Claparède, 1870

guttata Claparède, 1870a: 461, pl. 9 fig. 2. [*Eulalia* (*Eumida*)]
Eulalia (*Eumida*) *guttata* Claparède, 1870 nomen dubium

lactea Claparède, 1868: 553, pl. 18 fig. 2. [*Eteone*]
Hypereteone lactea (Claparède, 1868)

limbata Claparède, 1868: 558, pl. 17 fig. 6. [*Eulalia* (*Pterocirrus*)]
Pterocirrus limbatus (Claparède, 1868)

lineata Claparède, 1870a: 458, pl. 9 fig. 4. [*Anaitis*]
Phyllodoce lineata (Claparède, 1870)

marginata Claparède, 1868: 559, pl. 18 fig. 1. [*Eulalia* (*Pterocirrus*)]
Pterocirrus marginatus (Claparède, 1868)

microcephala Claparède, 1870a: 462, pl. 9 fig. 3. [*Eulalia* (*Pterocirrus*)]
Pterocirrus microcephalus (Claparède, 1870) nomen dubium

microceros Claparède, 1868: 557, pl. 16 fig. 4. [*Eulalia* (*Eumida*)]
A junior synonym of *Eumida viridis* (Linnaeus, 1767)

pallida Claparède, 1868: 556, pl. 16 fig. 6. [*Eulalia* (*Eumida*)]
A junior synonym of *Eumida sanguinea* (Örsted, 1843)

pancerina Claparède, 1870a: 456, pl. 9 fig. 1. [*Phyllodoce*]
A junior synonym of *Nereiphylla paretti* Blainville, 1828

parasitica Claparède & Panceri, 1867: 5-8. [*Alciopina*]
Alciopina parasitica Claparède & Panceri, 1867

peremptoria Claparède, 1870a: 459, pl. 9 fig. 6. [*Anaitis*]
Paranaitis peremptoria (Claparède, 1870) nomen dubium

pusilla Claparède, 1870a: 460, pl. 9 fig. 5. [*Anaitis*]
Nereiphylla pusilla (Claparède, 1870)

velifera Claparède, 1868: 560, pl. 17 fig. 2. [*Eulalia* (*Pterocirrus*)]
A junior synonym of *Pterocirrus macroceros* (Grube, 1860)

Family Polynoidae

fragile Claparède, 1868: 383, pl. 5 fig. 2. [*Hermadion*]
A junior synonym of *Subadyte pellucida* (Ehlers, 1864)

laevigata Claparède, 1870a: 378, pl. 1 fig. 2. [*Polynoe*]
A junior synonym of *Harmothoe spinifera* (Ehlers, 1864)

reticulata Claparède, 1870a: 374, pl. 1 fig. 1. [*Polynoe*]
Harmothoe reticulata (Claparède, 1870)

torquata Claparède, 1868: 378, pl. 2 fig. 3 [*Polynoe*]
A junior synonym of *Harmothoe spinifera* (Ehlers, 1864)

vasculosa Claparède, 1870a: 376, pl. 1 fig. 4. [*Polynoe*]
Polynoe vasculosa Claparède, 1870

Family Sabellidae

Amphiglena, Claparède, 1864: 492.
Amphiglena, Claparède, 1864

Dialychone Claparède, 1869: 169.
Dialychone Claparède, 1869

Fabricia (*Amphicorina*) Claparède, 1864: pl. 3 fig. 2.
Amphicorina Claparède, 1864

Leptochone Claparède, 1870a: 513.
A junior synonym of *Myxicola* Koch in Renier, 1847

acustica Claparède, 1869: 170, pl. 30 fig. 3. [*Dialychone*]
Dialychone acustica Claparède, 1869

aesthetica Claparède, 1870a: 514, pl. 14 fig. 1. [*Leptochone*]
Myxicola aesthetica (Claparède, 1870)

armandi Claparède, 1864: 492-196, pl. 3 fig. 1. [*Amphiglena*]
A junior synonym of *Amphiglena mediterranea* (Leydig, 1851)

armandi Claparède, 1864: 496, pl. 3 fig. 2. [*Fabricia* (*Amphicorina*)]
Amphicorina armandi (Claparède, 1864)

branchychona Claparède, 1870a: 503, pl. 14 fig. 5. [*Sabella*]
A junior synonym of *Parasabella saxicola* (Grube, 1861)

koellikeri Claparède, 1869: 163, pl. 22 fig. 4. [*Branchiomma*]
A junior synonym of *Acromegalomma lanigerum* (Grube, 1846)

salmacidis Claparède, 1869: 167, pl. 24 fig. 4. [*Laonome*]
Euratella salmacidis (Claparède, 1869)

vesiculosum neapolitana Claparède, 1869: 164, pl. 22 fig. 5. [*Branchiomma*]
A junior synonym of *Acromegalomma lanigerum* (Grube, 1846)

vigilans Claparède, 1870a: 501, pl. 14 fig. 3. [*Branchiomma*]
Megalomma vigilans (Claparède, 1870)

Family Serpulidae

aedificatrix Claparède, 1870a: 519, pl. 12 fig. 1. [*Salmacina*]
A junior synonym of *Salmacina dysteri* (Huxley, 1855)

coecus Claparède, 1870a: 517, pl. 13 fig. 4. [*Psygmobranchus*]
Protula coecus (Claparède, 1870) taxon inquirendum

crater Claparède, 1870a: 525, pl. 13 fig. 2. [*Serpula*]
A junior synonym of *Serpula vermicularis* Linnaeus, 1767

incrustans Claparède, 1869: 176, pl. 30 fig. 5. [*Salmacina*]
Salmacina incrustans Claparède, 1869

lunulifer Claparède, 1869: 181, pl. 31 fig. 3. [*Eupomatus*]
A junior synonym of *Hydroides dirampha* Mörch, 1863

militaris Claparède, 1869: 184, pl. 16 fig. 5. [*Pileolaria*]
Pileolaria militaris Claparède, 1869

multicostatus Claparède, 1869: 175, pl. 30 fig. 6. [*Psygmobranchus*]
A junior synonym of *Vermiliopsis infundibulum* (Philippi, 1844)

trypanon Claparède, 1870a: 527, pl. 14 fig. 4. [*Eupomatus*]
A junior synonym of *Hydroides norvegica* Gunnerus, 1768

Family Sigalionidae

Lepidopleurus Claparède, 1868: 415.
A junior homonym replaced by *Claparedepelogenia* Pettibone, 1997

ctenolepis Claparède, 1868: 398, pl. 4 fig. 1, pl. 6 fig. 2. [*Sthenelais*]
A junior synonym of *Sthenelais boa* (Johnston, 1833)

dendrolepis Claparède, 1868: 408, pl. 4 fig. 4, pl. 5 fig. 1. [*Sthenelais*]
A junior synonym of *Euthalalenessa oculata* (Peters, 1854)

fuliginosa Claparède, 1868: 404, pl. 4 fig. 2. [*Sthenelais*]
A junior synonym of *Sthenelais boa* (Johnston, 1833)

inclusus Claparède, 1868: 415, pl. 6 fig. 4. [*Lepidopleurus*]
Claparedepelogenia inclusus (Claparède, 1868)

leiolepis Claparède, 1868: 406, pl. 4 fig. 3, pl. 6 fig. 1. [*Sthenelais*]
A junior synonym of *Sthenelais limicola* (Ehlers, 1864)

synophthalmica Claparède, 1868: 389, pl. 3 fig. 1. [*Pholoe*]
A junior synonym of *Pholoe inornata* Johnston, 1839

Family Spionidae

Aonides Claparède, 1864: 505.
Aonides Claparède, 1864

Pygospio Claparède, 1863: 37.
Pygospio Claparède, 1863

agassizii Claparède, 1869: 54, pl. 22 fig. 1. [*Polydora*]
A junior synonym of *Polydora ciliata* (Johnston, 1838)

antennata Claparède, 1869: 60, pl. 21 fig. 3. [*Polydora*]
Pseudopolydora antennata (Claparède, 1869)

auricularius Claparède, 1864: 505, pl. 3 fig. 3. [*Aonides*]
A junior synonym of *Aonides oxycephala* (Sars, 1862)

auriseta Claparède, 1869: 71, pl. 24 fig. 2. [*Nerine*]
Scolelepis auriseta (Claparède, 1869) nomen dubium

elegans Claparède, 1863: 37, pl. 14 figs 17-21. [*Pygospio*]
Pygospio elegans Claparède, 1863

flava Claparède, 1870a: 487. [*Polydora*]
Diplolydora flava (Claparède, 1870)

fuliginosus Claparède, 1869: 62, pl. 23 fig. 1. [*Spio*]
Malacoceros fuliginosus (Claparède, 1869)

hoplura Claparède, 1869: 58, pl. 22 fig. 2. [*Polydora*]
Polydora hoplura Claparède, 1869

malmgreni Claparède, 1869: 73, pl. 22 fig. 3. [*Prionospio*]
Prionospio malmgreni Claparède, 1869 taxon inquirendum [indeterminable]

mecznikowianus Claparède, 1869: 64, pl. 23 fig. 2. [*Spio*]
Microspio mecznikowianus (Claparède, 1869)

sarsiana Claparède, 1869: 70, pl. 21 fig. 4. [*Nerine*]
A junior synonym of *Scolelepis foliosa* (Audouin & Milne Edwards, 1833)

Family Syllidae

Anoplosyllis Claparède, 1868: 524.
Anoplosyllis Claparède, 1868

Autolytus (*Stephanosyllis*) Claparède, 1864: 567.
A junior synonym of *Proceraea* Ehlers, 1864

Heterosyllis Claparède, 1863: 44.
Heterosyllis Claparède, 1863 nomen dubium

Microsyllis Claparède, 1863: 42.
A junior synonym of *Exogone* Örsted, 1845

Odontosyllis Claparède, 1863: 47.
Odontosyllis Claparède, 1863

Paedophylax Claparède, 1868: 520.
A junior synonym of *Exogone* Orsted, 1845

Polymastus Claparède, 1864: 569.
A junior synonym of *Eurysyllis* Ehlers, 1864

Pterosyllis Claparède, 1863: 46.
A junior synonym of *Amblyosyllis* Grube, 1857

Spermosyllis Claparède, 1864: 552.
A junior synonym of *Exogone* Örsted, 1845

Sphaerosyllis Claparède, 1863: 45.
Sphaerosyllis Claparède, 1863

Sylline Claparède, 1864: 550.
Exogone (*Sylline*) Claparède, 1864

Trypanosyllis Claparède, 1864: 558.
Trypanosyllis Claparède, 1864

armandi Claparède, 1864: 530, pl. 5 fig. 1. [*Syllis*]
A junior synonym of *Syllis prolifera* Krohn, 1852

armoricanus Claparède, 1863: 39, pl. 13 figs 21-23, 25-27. [*Syllis*]
A junior synonym of *Syllis variegata* Grube, 1860

aurantica Claparède, 1868: 529, pl. 15 fig. 1. [*Proceraea*]
Proceraea aurantica Claparède, 1868

aurantica Claparède, 1868: 510, pl. 14 fig. 3, pl. 13 fig. 5. [*Syllis*]
A junior synonym of *Syllis variegata* Grube, 1860

aurita Claparède, 1864: 539, pl. 5 fig. 5. [*Syllis*]
A junior synonym of *Syllis vittata* Grube, 1840

bacilligera Claparède, 1868: 508, pl. 14 fig. 4. [*Syllis*]
Syllis bacilligera Claparède, 1868 nomen dubium

brachiata Claparède, 1863: 44-45, pl. 13 fig. 35. [*Heterosyllis*]
Heterosyllis brachiata Claparède, 1863

brevicirrata Claparède, 1863: 42, pl. 12 figs 1-2. [*Microsyllis*]
Exogone brevicirrata (Claparède, 1863) nomen dubium

brevipes Claparède, 1864: 551, pl. 6 fig. 4. [*Sylline*]
Exogone (*Sylline*) *brevipes* (Claparède, 1864)

clavata Claparède, 1863: 41, pl. 13 figs 28-29. [*Syllis*]
Salvatoria clavata (Claparède, 1863)

claviger Claparède, 1868: 521, pl. 13 fig. 2. [*Paedophylax*]
Exogone claviger (Claparède, 1868)

coeliaca Claparède, 1868: 513, pl. 13 fig. 3. [*Trypanosyllis*]
Trypanosyllis (*Trypanosyllis*) *coeliaca* Claparède, 1868

ctenostoma Claparède, 1868: 512, pl. 12 fig. 4. [*Odontosyllis*]
Odontosyllis ctenostoma Claparède, 1868

dorsigera Claparède, 1864: 560, pl. 7 fig. 1. [*Pterosyllis*]
A junior synonym of *Amblyosyllis spectabilis* (Johnston, 1865)

dugesiana Claparède, 1864: 556, pl. 8 fig. 2. [*Odontosyllis*]
Odontosyllis dugesiana Claparède, 1864

edentula Claparède, 1868: 524, pl. 12 fig. 2. [*Anoplosyllis*]
Anoplosyllis edentula Claparède, 1868

erinaceus Claparède, 1863: 45, pl. 13 fig. 38. [*Sphaerosyllis*]
Erinaceusyllis erinaceus (Claparède, 1863)

formosa Claparède, 1863: 46, pl. 13 figs 30-31. [*Pterosyllis*]
A junior synonym of *Amblyosyllis spectabilis* (Johnston, 1865)

gibba Claparède, 1863: 47, pl. 12 figs 7-8. [*Odontosyllis*]
Odontosyllis gibba Claparède, 1863

hamata Claparède, 1868: 505, pl. 15 fig. 2. [*Syllis*]
A junior synonym of *Haplosyllis spongicola* (Grube, 1855)

hesperidium Claparède, 1868: 526, pl. 14 fig. 4. [*Autolytus*]
Myrianida hesperidium (Claparède, 1868)

hexagonifera Claparède, 1864: 533, pl. 5 fig. 2. [*Syllis*]
A junior synonym of *Syllis variegata* Grube, 1860

hystrix Claparède, 1863: 45, pl. 13 figs 36-37. [*Sphaerosyllis*]
Sphaerosyllis hystrix Claparède, 1863

kefersteinii Claparède, 1863: 42, pl. 12 figs 3-6. [*Exogone*]
A junior synonym of *Exogone naidina* Örsted, 1845

krohnii Claparède, 1864: 558, pl. 7 fig. 2. [*Trypanosyllis*]
Trypanosyllis krohnii Claparède, 1864

limbata Claparède, 1868: 518, pl. 13 fig. 4. [*Grubea*]
Salvatoria limbata (Claparède, 1868)

maculata Claparède, 1868: 532, pl. 13 fig. 1. [*Myrianida*]
A junior synonym of *Myrianida pinnigera* (Montagu, 1808)

normannica Claparède, 1863: 40, pl. 13 fig. 24. [*Syllis*]
A junior synonym of *Nudisyllis divaricata* (Keferstein, 1862)

paradoxus Claparède, 1864: 569, pl. 8 fig. 3. [*Polymastus*]
A junior synonym of *Eurysyllis tuberculata* Ehlers, 1864

pirifera Claparède, 1868: 515, pl. 14 fig. 2. [*Sphaerosyllis*]
Sphaerosyllis pirifera Claparède, 1868

roseus Claparède, 1864: 566, pl. 7 fig. 4. [*Autolytus*]
Myrianida roseus (Claparède, 1864) nomen dubium

rubrovittatus Claparède, 1864: 563, pl. 7 fig. 3. [*Autolytus*]
Myrianida rubrovittatus Claparède, 1864 nomen dubium

scapularis Claparède, 1864: 567, pl. 7 fig. 5. [*Autolytus* (*Stephanosyllis*)]
Proceraea scapularis (Claparède, 1864)

simillima Claparède, 1864: 537, pl. 5 fig. 4. [*Syllis*]
A junior synonym of *Syllis hyalina* Grube, 1863

tenuicirrata Claparède, 1864: 547, pl. 6 fig. 2. [*Sphaerosyllis*]
Salvatoria tenuicirrata (Claparède, 1864)

torulosa Claparède, 1864: 553, pl. 6 fig. 5. [*Spermosyllis*]
Exogone (*Exogone*) *torulosa* (Claparède, 1864)

veruger Claparède, 1868: 523, pl. 12 fig. 3. [*Paedophylax*]
Exogone veruger (Claparède, 1868)

Family Terebellidae

ambigrada Claparède, 1869: 142, pl. 18 fig. 6. [*Phenacia*]
A junior synonym of *Thelepus cincinnatus* (Fabricius, 1780)

caliendrum Claparède, 1869: 146, pl. 29 fig. 2. [*Polycirrus*]
Polycirrus caliendrum Claparède, 1869

flavescens Claparède, 1869: 136, pl. 23 fig. 6. [*Terebella*]
A junior synonym of *Eupolymnia nesidensis* (delle Chaije, 1828)

incana Claparède, 1870a: 493, pl. 13, fig 6. [*Amphitrite*]
A junior synonym of *Amphitrite rubra* (Risso, 1826)

laevirostris Claparède, 1869: 139, pl. 9 fig. 5. [*Terebella*]
A junior synonym of *Amphitritides gracilis* (Grube, 1860)

nucleolata Claparède, 1869: 141, pl. 18 fig. 8. [*Heterophenacia*]
Thelepus nucleolata (Claparède, 1869)

retrograda Claparède, 1869: 143, pl. 28 fig. 7. [*Phenacia*]
A junior synonym of *Thelepus cincinnatus* (Fabricius, 1780)

sanguinea Claparède, 1869: 128, pl. 30 fig. 1, pl. 29 fig. 3. [*Heteroterebella*]
A junior synonym of *Terebella lapidaria* Linnaeus, 1767

sulcigera Claparède, 1869: 140, pl. 18 fig. 5. [*Terebella*]
A junior synonym of *Terebella lapidaria* Linnaeus, 1767

vestita Claparède, 1869: 137, pl. 9 fig. 4. [*Terebella*]
A junior synonym of *Nicolea venustula* (Montagu, 1819)

Phylum Arthropoda

Class Hexanauplia
Family Clausiidae

Clausia Claparède, 1863: 94.
Clausia Claparède, 1863

lubbockii Claparède, 1863: 94, pl. 18 figs 7-11. [*Clausia*]
Clausia lubbockii Claparède, 1863

Family Lamippidae

proteus Claparède, 1867: 23-28, pl. 5. [*Lamippe*]
Lamippe proteus Claparède, 1867

Family Monstrillidae

danae Claparède, 1863: 95, pl. 16 figs 1-6. [*Monstrilla*]
A junior homonym replaced by *Cymbasoma thompsonii* (Giesbrecht, 1893)

Family Sabelliphilidae

sarsii Claparède, 1870b: 10-18, pl. 7. [*Sabelliphilus*]
Sabelliphilus sarsii Claparède, 1870

Class Pycnogonida
Family Phoxichilididae

cheliferum Claparède, 1863: 103, pl. 18 fig. 12. [*Phoxichilidium*]
Phoxichilidium cheliferum Claparède, 1863 nomen dubium

Phylum Entoprocta

Family Loxosomatidae

kefersteinii Claparède, 1867: 28-34, pl. 6. [*Loxosoma*]
Loxomitra kefersteinii (Claparède, 1867)

Phylum Gastroticha

Family Thaumastodermatidae

Hemidasys Claparède, 1867: 16-23, pl. 4 figs 5-9.
Hemidasys Claparède, 1867

agaso Claparède, 1867: 16-23, pl. 4 figs 5-9. [*Hemidasys*]
Hemidasys agaso Claparède, 1867

Phylum Kinorhyncha

Class Cyclorhagida
Family Echinoderidae

Echinoderes Claparède, 1863: 90, pl. 16 figs 7-16.
Echinoderes Claparède, 1863

dujardinii Claparède, 1863: 90-93, pl. 16 figs 7-16. [*Echinoderes*]
Echinoderes dujardinii Claparède, 1863

Phylum Nematoda

Class Chromadorea
Family Desmoscolecidae

Desmoscolex Claparède, 1863: 89.
Desmoscolex Claparède, 1863

minutus Claparède, 1863: 89, pl. 18 figs 1-7. [*Desmoscolex*]
Desmoscolex minutus Claparède, 1863

Family Draconematidae

Chaetosoma Claparède, 1863: 88.
A junior homonym replaced by *Draconema* Cobb, 1913

ophicephalum Claparède, 1863: 88, pl. 18 figs 2-3. [*Chaetosoma*]
Draconema ophicephalum (Claparède, 1863)

Phylum Nemertina

Class Hoplonemertea
Family Oerstediidae

marmoratum Claparède, 1863: 24, pl. 5 fig. 14. [*Tetrastemma*]
A junior synonym of *Oerstedia dorsalis* (Abildgaard in Müller, 1806) (nomenclature follows McCaul, 1963)

Phylum Platyhelminthes

Family Cercyridae

dioica Claparède, 1863: 18, pl. 3 figs 7-11. [*Planaria*]
Sabussowia dioica (Claparède, 1863)

Family Cylindrostomidae

Enterostomum Claparède, 1861: 135.
Enterostomum Claparède, 1861 nomen oblitum

fingalianum Claparède, 1861: 135-137, pl. 6 figs 11-13. [*Enterostomum*]
Cylindrostoma fingalianum (Claparède, 1861)

Family Euryleptidae

aurita Claparède, 1861: 144-146, pl. 7 figs 5-10. [*Eurylepta*]
Oligocladus auritus (Claparède, 1861)

Family Leptoplanidae

mertensii Claparède, 1861: 147-148, pl. 7 figs 11-12. [*Centrostomum*]
Leptoplana mertensi (Claparède, 1861) nomen dubium

Family Macrostomidae

schultzii Claparède, 1863: 15, pl. 4 figs 1-2. [*Macrostomum*]
Omalostomum schultzii (Claparède, 1863)

Family Polycystididae

caledonicum Claparède, 1861: 132-134, pl. 5 fig. 5. [*Prostomum*]
Acrorhynchides caledonicum (Claparède, 1861)

kefersteinii Claparède, 1863: 16, pl. 3 figs 1-6. [*Prostomum*]
A junior synonym of *Polycystis naegelii* Kölliker, 1845

Family Provorticidae

hispidus Claparède, 1863: 15, pl. 4 fig. 1. [*Vortex*]
Provortex hispidus (Claparède, 1863)

incertae sedis

Onchogaster Claparède: 1863: 13. (Not listed in WoRMS)

natator Claparède: 1863: 13, pl. 5 figs 1-4. [*Onchogaster*] (Not listed in WoRMS)

pachycera Claparède, 1863: 12-13, pl. 18 fig. 1. [*Cercaria*] (Not listed in WoRMS)

Phylum Rotifera (nomenclature follows Jersabek & Leitner, 2013)

Class Eurotatoria
Family Dicranophoridae

Balatro Claparède, 1867: 12-16, pl. 4, figs 3-4.
Balatro Claparède, 1867

calvus Claparède, 1867: 12-16, pl. 4. [*Balatro*]
Balatro calvus Claparède, 1867

Phylum Xenacoelomorpha

Family Nadinidae

minuta Claparède, 1863: 18, pl. 5 fig. 8. [*Convoluta*]
Nadina minuta Claparède, 1863

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Shallow water turrids of Ile des Pins, New Caledonia (Mollusca, Gastropoda)

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Abstract: The marine malacofauna of New Caledonia is among the most studied and best known of the Indo-Pacific region. Previous studies have shown that its richness and species compositions are examples of extreme spatial heterogeneity. Turrids are among the richest and most diverse groups of marine gastropods. In the present paper the shallow-water turrid fauna of Ile des Pins is inventoried for the first time. 174 morphotypes hosted in 8 families are herein recorded, of which 22 species are considered new records for New Caledonia. The following new combinations were introduced: *Mitromorpha drivasi* (Chang, 1995), *Acrista nana* (Hervier, 1896), *Acrista latirella* (Melvill & Standen, 1896), *Acrista pusilla* (Dunker, 1871), *Acrista tuberculifera* (Hervier, 1896), *Hemilienardia idiomorpha* (Hervier, 1897), *Heterocithara diatula* (Hervier, 1897), *Heterocithara isophanes* (Hervier, 1897), and *Pseudorhaphitoma hervieri* Hedley, 1922.

Keywords: New Caledonia - inventory - Drilliidae - Pseudomelatomidae - Horaiclavidae - Turridae - Mitromorphidae - Clathurellidae - Raphitomidae - Mangeliidae.

INTRODUCTION

The turrids (s.l.), consist of a set of families previously classified in the family Turridae (Powell, 1966). Following a large phylogenetic study, Puillandre *et al.* (2011) assigned species of this family into 13 distinct families. Despite this improvement in higher level taxonomy, a considerable proportion of turrids have never been authoritatively reported since their original description. As a result, many species have never been assigned to modern genera.

In addition to the taxonomic problems, almost nothing is known about regional diversity of turrids and the differences in faunal assemblages of different regions. An exception might be New Caledonia (including the Loyalty Islands), which is the type locality of many turrid species and which has witnessed a number of incomparable marine sampling expeditions performed by the MNHN to Koumac, Touho, and Lifou. Based on these expeditions, a total of 504 turrid morphotypes were recorded, of which 231 were identified to species level (Bouchet in Payri & Richer de Forges, 2007). A study of recently published taxonomic literature demonstrated that at least 25 additional species have been described subsequently from New Caledonia (Fedosov & Puillandre, 2012; Kilburn *et al.*, 2014; Morassi *et al.*, 2017; Fedosov *et al.*, 2017; Kantor *et al.*, 2017; Fedosov & Puillandre, 2020).

A comparison of the turrid species composition of these three sites has revealed a very high level of heterogeneity between sites, with only 21% of species overlap (Philippe Bouchet, unpublished pers. communication). Since the previously sampled areas are in the northern part of New Caledonia (Koumac and Touho) and the Loyalty Islands, the aim of the present paper is the documentation of the shallow-water turrid fauna of the southernmost part of New Caledonia, the Isle des Pins.

MATERIALS AND METHODS

Sand grit was collected in preferential spots such as overhangs, caves and tunnels where specimens tend to accumulate. Sampled material was washed in fresh water, dried in thin mesh bags and sieved into different fractions (<1 mm, 1-2.5 mm, 2.5-5 mm, 5 mm-1 cm and >1 cm). Approximately 20 kg of material was collected at Ile des Pins, among which half (the fractions larger than 5 mm and smaller than 1 mm) were sorted on site. Remaining material was sorted mostly under a dissecting microscope at MHNG. When needed, the specimens have been cleaned with mounted needles and/or ultrasonic apparatus. The seldomly live collected specimens were preserved in 90% ethanol.

All dives were oraganized through the Kunié Diving resort at regular dive localities. Due to poor weather

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conditions, sites were determined by vessel operators based on their accessibility, and therefore were limited to the most protected and closest dive spots from the resort harbour. All diving stations data (dates, collector names, minimum and maximum depth, precise GPS positions, habitats and eventual additional notes) were consistently recorded.

A six day collection trip in February 2019 sampled 11 stations across 8 sites ranging from a depth of 0.5-27 m. See Annex 1 for stations map and Annex 2 for stations GPS positions.

Specimen images were captured through a Canon 90D with an MP-E 65 mm 1-5x lens mounted on a stack shot rail. Raw images were then stacked with Zerene stacker and final editing was completed in GIMP.

Specimen identifications were based on original descriptions, comparisons with type material, or with well documented specimen vouchers. Type material specimens, type pictures or voucher specimens were obtained from MNHN, MHNBx, ANSP, NHMUK, AMS, NSMT, and from the late Dr Richard Kilburn. Each specimen was directly compared with illustrated morphotypes from an unpublished catalogue of samplings from Koumac, Touho and Lifou (unpublished data, MNHN), in order to complete the southern New Caledonian faunal list presented here.

The classification of conoideans adapted by Bouchet *et al*. (2011) is followed. Generic assignments were generally followed from accepted opinions in WoRMS (2022), in a few cases, the introduction of new combination was necessary. Plates are arranged by species morphology with similar characteristics prevailing over alphabetic order.

The qualifier "aff.", meaning "species affinis" is used for morphospecies that are clearly distinguishable but close to known taxa. The appendix "cf." meaning "confer" is used in cases where morphospecies might be conspecific with known species but some doubts remain.

If obsolete geographical names and measure units are given in the type locality, modern references are provided in square brackets "[ ]".

Abbreviations

AMS	Australian Museum of Sydney
ANSP	Academy of Natural Sciences of Philadelphia
idp	Ile des Pins
MHNBx	Muséum d'Histoire Naturelle de Bordeaux
MHNG	Muséum d'Histoire Naturelle de Genève
MNHN	Muséum National d'Histoire Naturelle, Paris
NHMUK	Natural History Museum, London
NSMT	National Museum of Nature and Science (Japan)

RESULTS

In total, 2252 turrid specimens (or identifiable parts of specimens) were segregated into 174 morphotypes in 8 families. With 72 species, the family Raphitomidae was found to be the most diverse, while Pseudomelatomidae was the least diverse turrid family with only a single recorded species.

From those 174 morphotypes, 102 were recognized as described species, 35 were only assigned to genus level and are presumed to be new to science while the other 37 remaining morphotypes are similar to described species but are too poor in quality or represented by too few specimens to be sure. 46 morphotypes were represented by only a single specimen and 34 by two specimens, respectively, demonstrating that our sampling is far away from saturation, and that rare species make up an important part of the local turrid diversity. In contrast, *Anarithma metula* (though, it might represent a species complex) was represented by a total of 218 specimens. *Microdaphne morrisoni* and *Heterocithara strombillum*, secondarily were represented by more than 150 specimens each and were found at all stations sampled.

A comparison of the morphotypes found at Ile des Pins with those collected during the expeditions to Touho, Koumac and Lifou (MNHN unpublished catalogue of the New Caledonian turrid morphotypes), revealed that a total of 28 morphotypes were exclusively collected at Ile des Pins. However, since 6 species out of these 28 morphotypes were originally described from New Caledonia, 22 species are considered new records for New Caledonia. An additional 21 species would require a close examination and comparison to specimens collected at the other sites in order to confirm whether they are conspecific or not.

In the following list most morphotypes identified to genus level only have a number after "sp." These numbers do not refer a numbering of unidentified morphotypes found in the present work, but to an unpublished, temporary numbering system of all species used by the authors in their research. Additionally, specimens demarcated with proceeding letters indicate strong affinities to the numerical destinctions.

Family Drilliidae Olsson, 1964

12 morphotypes

Genus *Clavus* Montfort, 1810

Type species: *Clavus flammulatus* Montfort, 1810 (type by original designation). Type locality: unknown.

Clavus bilineatus (Reeve, 1845)

Plate 1, fig. 1

Pleurotoma bilineata Reeve, 1845.

Type locality: 15 fm [27 m], Capul and Mindoro Islands, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp3.2, idp6.

Clavus formosus (Reeve, 1846)

Plate 1, fig. 5

Pleurotoma formosa Reeve, 1846.

Type locality: Capul Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp6.

Clavus lamberti (Montrouzier, 1860)

Plate 1, fig. 2

Pleurotoma lamberti Montrouzier, 1860.

Type locality: Art Island, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp5, idp6, idp7, idp8.

Clavus aff. *lamberti* (Montrouzier, 1860)

Plate 1, fig. 3

Material examined: New Caledonia, Ile des Pins: st. idp1.

Remarks: Known from a single worn specimen, which is similar to *Clavus lamberti*, but differs in having fewer axial ribs. This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Clavus moquinianus (Montrouzier, 1874)

Plate 1, fig. 9

Pleurotoma moquiniana Montrouzier in Souverbie & Montrouzier, 1874.

Type locality: Art Island, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp5, idp6, idp7.

Remarks: That species was not recorded in the unpublished MNHN catalogue of morphotypes, but was originally described from New Caledonia and is recorded from New Caledonia in Kilburn *et al*. (2014).

Clavus pica Reeve, 1843

Plate 1, fig. 7

Pleurotoma pica Reeve, 1843.

Type locality: Capul Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp5.2.

Clavus picoides Kilburn, Fedosov & Kantor, 2014

Plate 1, fig. 8

Clavus picoides Kilburn, Fedosov & Kantor, 2014.

Type locality: Stn. 1352, 22°22.2'S, 166°16.0-166°16.1'E; 27-35 m, Grand Récif Aboré outer slope, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp3.2, idp5.2.

Clavus virginieae Kilburn, Fedosov & Kantor, 2014

Plate 1, fig. 4

Clavus virginieae Kilburn, Fedosov & Kantor, 2014.

Type locality: Stn. 1455, 20°56.8'S, 167°02.7'E; 15-20 m, Baie du Santal, between Cap Wekutr and Cap Wajez, Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp5, idp5.2, idp6, idp7.

Genus *Iredalea* Oliver, 1915

Type species: *Iredalea subtropicalis* W. R. B. Oliver, 1915 (type by original designation). Type locality: Sunday Island [Raoul Island], Kermadec Islands.

Iredalea balteata (Gould, 1860)

Plate 1, fig. 11

Columbella (Anachis) *balteata* Gould, 1860.

Type locality: China Sea.

Material examined: New Caledonia, Ile des Pins: st. idp3, idp4.

Iredalea cf. *balteata* (Gould, 1860)

Plate 1, fig. 12

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp7, idp8.

Remarks: The specimens differ from typical *Iredalea balteata* in having more prominent nodule-like axial ribs and two rows of white spots on the brown band below periphery. More research is necessary to determine whether this is a case of polymorphism within one species, or if there is justification for a more speciose complex.

Iredalea inclinata (Sowerby III, 1893)
Plate 1, fig. 6

Pleurotoma inclinata G. B. Sowerby III, 1893.

Type locality: Mauritius.

Material examined: New Caledonia, Ile des Pins: st. idp5, idp6, idp7.

Genus *Plagiostropha* Melvill, 1927

Type species: *Plagiostropha quintuplex* Melvill, 1927 (type by monotypy). Type locality: unknown.

Plagiostropha sp.
Plate 1, fig. 10

Material examined: New Caledonia, Ile des Pins: st. idp7.

Family Pseudomelatomidae J. P. E. Morrison, 1966

1 morphotype.

Genus *Crassispira* Swainson, 1840

Type species: *Pleurotoma bottae* Valenciennes in Kiener, 1839 accepted as *Crassispira bottae* (Valenciennes in Kiener, 1839) (type by subsequent designation). Type locality: Mazatlán, M. Botta.

Crassispira scala Kantor *et al.*, 2017
Plate 2, fig. 13

Crassispira scala Kantor, Stahlschmidt, Aznar-Cormano, Bouchet & Puillandre, 2017.

Type locality: st. PR159, 05°07.1′S, 145°49.4′E; 15 m, N. Wonad I., Madang Lagoon, Papua-New Guinea.

Material examined: New Caledonia, Ile des Pins: st. idp5, idp5.2, idp6.

Family Horaiclavidae Bouchet *et al.*, 2011

15 morphotypes.

Genus *Anacithara* Hedley, 1922

Type species: *Mangelia naufraga* Hedley, 1909 accepted as *Anacithara naufraga* (Hedley, 1909) (type by original designation). Type locality: Hope Island, Queensland, Australia.

Anacithara cf. *lita* (Melvill & Standen, 1896)
Plate 2, fig. 23

Clathurella lita Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp7, idp8.

Remarks: The present species is most probably conspecific with *Anacithara lita* (Melvill & Standen, 1896), but specimens with intact protoconchs are needed to be sure.

Anacithara cf. *stricta* Hedley, 1922
Plate 2, fig. 27

Anacithara stricta Hedley, 1922.

Type locality: 17 to 20 fm. [31-37 m], Mast Head Island, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp5.2.

Remarks: The present specimens appear to be *Anacithara stricta* Hedley, 1922. However, the type of the latter species is in such poor quality that fresh examples from the type locality are needed for comparison. This morphotype was not recorded among the specimens collected and documented by the unpublished MNHN catalogue of morphotypes.

Anacithara themeropis (Melvill & Standen, 1896)
Plate 2, fig. 26

Drillia themeropis Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2.

Anacithara conata (Hedley, 1909)
Plate 2, fig. 25

Mangelia naufraga var. *conata* Hedley, 1909.

Type locality: Hope Island, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2.

Anacithara sp.3
Plate 2, fig. 24

Material examined: New Caledonia, Ile des Pins: st. idp5.2, idp6.

Genus *Carinapex* Dall, 1924

Type species: *Drillia minutissima* Garrett, 1873 (as a subgenus of *Daphnobela* Cossmann, 1896) accepted as *Carinapex minutissima* (Garrett, 1873) (type by original designation). Type locality: Viti Isles [Fiji].

Carinapex amirowlandae Wiedrick, 2015

Plate 2, fig. 15

Carinapex amirowlandae Wiedrick, 2015.

Type locality: 100-250 m, North Central Punta Engano, Mactan Island, Cebu Province, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Carinapex chaneyi Wiedrick, 2015

Plate 2, fig. 17

Carinapex chaneyi Wiedrick, 2015.

Type locality: 8°39'S, 158°14'E; in rubble at 20-25 m off exposed side of Karunjou Island, off Marovo Lagoon, east side Vanguna Island, Solomon Islands.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp7.

Remarks: That species was erroneously identified as *Carinapex minutissima* in Bouchet *et al*. (2011).

Carinapex minutissima (Garrett, 1873)

Plate 2, fig. 16

Drillia minutissima Garrett, 1873.

Type locality: Viti Isles [Fiji].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Remarks: Based on the recent identification of *Carinapex chaneyi* (Wiedrick, 2015: 7) in Bouchet *et al*. (2011), *Carinapex minutissima* is here recognized from New Caledonia for the first time.

Carinapex mooreorum Wiedrick, 2015

Plate 2, fig. 18

Carinapex mooreorum Wiedrick, 2015.

Type Locality: 19°55' 3.28"N, 155°53'26.38"W; in tide pool rubble at -0.3 m, "Anaeho" Omalu Point, Kona North District, Hawaii.

Material examined: New Caledonia, Ile des Pins: st. idp7.

Carinapex philippinensis Wiedrick, 2015

Plate 2, fig. 14

Carinapex philippinensis Wiedrick, 2015.

Type locality: 11°29'0.12"N, 119°50'13.82"E; 150 m, Linapacan Island, Palawan Province, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp1.

Genus *Ceritoturris* Dall, 1924

Type species: *Crassispira bittium* Dall, 1924 accepted as *Ceritoturris bittium* (Dall, 1924) (type by original designation). Type locality: Hawaiian Islands.

Ceritoturris papillosa (Garrett, 1873)

Plate 2, fig. 21

Drillia papillosa Garrett, 1873.

Type locality: Viti Isles [Fiji].

Material examined: New Caledonia, Ile des Pins: st. idp3, idp3.2, idp5, idp6, idp7, idp8.

Ceritoturris theoteles (Melvill & Standen, 1896)

Plate 2, fig. 19

Mangilia (Glyphostoma) theoteles (Melvill & Standen, 1896).

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp5, idp5.2, idp7.

Remarks: *Carinapex cernohorskyi* Wiedrick, 2015 appears to be conspecific. *Carinapex theoteles* was described from the Loyalty Islands, but is recorded from Japan, French Polynesia, and Hawaii under the name *C. cernohorskyi* in Wiedrick (2015).

Ceritoturris cf. *theoteles* (Melvill & Standen, 1896)

Plate 2, fig. 20

Material examined: New Caledonia, Ile des Pins: idp7.

Remarks: The present species is very similar to *Carinapex theoteles* but differs in the rounded and similar-sized nodules of both spirals while in *C. theoteles*, the nodules of the abapical spiral row are much bigger and vertically elongated.

Ceritoturris sp.1

Plate 2, fig. 22

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp7.

Genus *Graciliclava* Shuto, 1983

Type species: *Graciliclava mackayensis* Shuto, 1983 accepted as *Graciliclava costata* (Hedley, 1922) (type by original designation). Type locality: 20°52'S / 149°29'E, 35 m, E of Mackay, Queensland, Australia.

Graciliclava costata (Hedley, 1922)

Plate 3, fig. 28

Clavus costatus Hedley, 1922.

Type locality: 12 fm [22 m], Darnley Island, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp3, idp5.2.

Family Turridae H. Adams & A. Adams, 1853 (1838)

8 morphotypes.

Genus *Iotyrris* Medinskaya & Sysoev, 2001

Type species: *Iotyrris marquesensis* Sysoev, 2002 (type by subsequent designation). Type locality: 9°44.6'S, 138°51.1'W; 115-120 m, Marquesas Islands, French Polynesia.

Iotyrris cingulifera (Lamarck, 1822)

Plate 3, fig. 36

Pleurotoma cingulifera Lamarck, 1822.

Type locality: unknown.

Material examined: New Caledonia, Ile des Pins: st. idp piscine.

Genus *Lophiotoma* T. L. Casey, 1904

Type species: *Pleurotoma tigrina* Lamarck, 1822 accepted as *Lophiotoma acuta* (Perry, 1811) (type by subsequent designation). Type locality: unknown.

Lophiotoma sp.

Plate 3, fig. 29

Material examined: New Caledonia, Ile des Pins: st. idp2.

Genus *Turridrupa* Hedley, 1922

Type species: *Pleurotoma acutigemmata* E. A. Smith, 1877 accepted as *Turridrupa acutigemmata* (E. A. Smith, 1877) (type by original designation). Type locality: unknown.

Turridrupa bijubata (Reeve, 1843)

Plate 3, fig. 33

Pleurotoma bijubata, Reeve, 1843.

Type locality: Under rocks, Bureas Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp3, idp5, idp8.

Turridrupa consobrina Powell, 1967

Plate 3, fig. 32

Turridrupa astricta consobrina Powell, 1967.

Type locality: 40-50 feet [12-15 m], Maalaea Bay, Maui Island, Hawaii.

Material examined: New Caledonia, Ile des Pins: st. idp5.2, idp7, idp8.

Turridrupa diffusa Powell, 1967

Plate 3, fig. 30

Turridrupa diffusa Powell, 1967.

Type locality: Samoa.

Material examined: New Caledonia, Ile des Pins: st. idp5.2, idp6.

Turridrupa cf. *jubata* (Hinds, 1843)

Plate 3, fig. 31

Pleurotoma jubata Hinds, 1843.

Type locality: In mud at 32.9 m, Straits of Malacca.

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: The present species differs from typical specimens of *Turridrupa jubata* (Hinds, 1843) by the smaller and more slender shape, the weaker spiral cords, and the less flared out anal sinus opening.

Genus *Xenuroturris* Iredale, 1929

Type species: *Xenuroturris legitima* Iredale, 1929 (type by original designation). Type locality: Michaelmas Cay, Queensland, Australia.

Xenuroturris legitima Iredale, 1929

Plate 3, fig. 35

Xenuroturris legitima Iredale, 1929.

Type locality: Michaelmas Cay, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp4.

Xenuroturris millepunctata **(G.B. Sowerby III, 1909)**
Plate 3, fig. 34

Pleurotoma millepunctata G. B. Sowerby III, 1909.

Type locality: Monac Island, New, Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp2.

Family Mitromorphidae T. L. Casey, 1904

16 morphotypes.

Genus *Lovellona* Iredale, 1917

Type species: *Conus atramentosus* Reeve, 1849 accepted as *Lovellona atramentosa* (Reeve, 1849) (type by original designation). Type locality: 25 fm [45.7 m], Mindoro Island, Philippines.

Lovellona atramentosa **(Reeve, 1849)**
Plate 4, fig. 37

Conus atramentosus Reeve, 1849.

Type locality: 25 fm [45.7 m], Mindoro Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp3.2, idp5, idp6, idp8.

Genus *Mitromorpha* Carpenter, 1865

Type species: *Daphnella filosa* Carpenter, 1864 accepted as *Mitromorpha carpenteri* Glibert, 1954 (type by monotypy). Type locality: Santa Barbara, California, USA.

Remarks: *Anarithma* Iredale, 1916 closely resembles *Mitromorpha* but can be distinguished by a swollen columella bearing a small v-shaped notch instead of folds. We agree with Chino & Stahlschmidt (2009) that the use of weakly distinguishable genera in such a species-rich and confusing group as the turrids is not recommended. Until studies based on molecular data are available, we assign all species to the genus *Mitromorpha* and omit *Anarithma*.

Mitromorpha alphonsiana **(Hervier, 1900)**
Plate 4, fig. 51

Columbella alphonsiana Hervier, 1900.

Type locality: Lifou. Loyalty Islands, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp8.

Mitromorpha drivasi **(Chang, 1995) n. comb.**
Plate 4, fig. 39

Anarithma drivasi Chang, 1995.

Type locality: Lüdao Islet, Taiwan.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp5.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Mitromorpha fischeri **(Hervier, 1900)**
Plate 4, fig. 40

Columbella fischeri Hervier, 1900.

Type locality: Lifou. Loyalty Islands, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp3, idp5, idp6, idp8.

Mitromorpha inornata **(Hervier, 1900)**
Plate 4, fig. 48

Columbella stepheni var. *inornata* Hervier, 1900.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp5.

Mitromorpha iozona **(Hervier, 1900)**
Plate 4, fig. 50

Columbella iozona Hervier, 1900.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp3, idp6.

Mitromorpha metula **(Hinds, 1843)**
Plate 4, figs 42-43

Clavatula metula Hinds, 1843.

Type locality: unknown.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Remarks: This species may represent a species complex and further genetic analysis is required to resolve its taxonomic position.

Mitromorpha salisburyi (Cernohorsky, 1978)

Plate 5, fig. 52

Mitrolumna salisburyi Cernohorsky, 1978.

Type locality: 32 fm [59 m], Maile Point, Oahu, Hawaii.

Material examined: New Caledonia, Ile des Pins: st. idp3, idp6.

Mitromorpha sublachryma (Hervier, 1900).

Plate 4, fig. 44

Columbella sublachryma Hervier, 1900.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp3.2, idp5, idp5.2, idp6, idp7.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes, but was originally described from Lifou, therefore it is not considered new to New Caledonia.

Mitromorpha cf. *sublachryma* (Hervier, 1900) morph 1

Plate 4, fig. 45

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Remarks: The present species differs from typical *Anarithma sublachryma* (Hervier, 1900) by the less developed axial sculpture, the two spiral grooves per whorl (compared to one in *Anarithma sublachryma)*, by the two pinkish cords on the upper suture and grooves, and by the large brown dorsal blotch on the final whorl.

Mitromorpha cf. *sublachryma* (Hervier, 1900) morph 2

Plate 4, fig. 46

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Remarks: The present morphotype differs from the typical *Anarithma sublachryma* (Hervier, 1900) by the faint axial sculpture, the almost smooth surface of the shell and by the more elongated and less biconical profile. This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Mitromorpha cf. *sublachryma* (Hervier, 1900) morph 3

Plate 4, fig. 47

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Remarks: The present morphotype differs from *Anarithma sublachryma* (Hervier, 1900) in being much more stout, with shorter whorls, relatively deeper spiral grooves, resulting in a rugose shell surface similar to that of *A. metula* (Hinds, 1843). This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Mitromorpha aff. *thalaoides* Chino & Stahlschmidt, 2014

Plate 5, fig. 53

Mitromorpha thalaoides Chino & Stahlschmidt, 2014.

Type locality: Baie du Santal, WSW of Pointe d'Easo, Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp5, idp8.

Remarks: The present morphotype differs from *Mitromorpha thalaoides* Chino & Stahlschmidt, 2014 by the ovate shape (instead of biconic), the larger adult size, the more numerous and finer knobs, and the completely different coloration.

Mitromorpha sp. 3

Plate 4, fig. 41

Material examined: New Caledonia, Ile des Pins: st. idp5, idp5.2.

Mitromorpha sp. 5

Plate 4, fig. 49

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Mitromorpha sp. 6

Plate 4, fig. 38

Material examined: New Caledonia, Ile des Pins: st. idp8.

Family Clathurellidae H. Adams & A. Adams, 1858

25 morphotypes.

Genus *Acrista* Hedley, 1922

Type species: *Lienardia punctilla* Hedley, 1922 accepted as *Acrista punctilla* (Hedley, 1922) (type by original designation). Type locality: 5 to 8 fathoms [9-15 m], Murray Island, Queensland, Australia.

Remarks: Described as a subgenus of *Lienardia*, we consider it a full genus being more similar to *Etrema* but differing in the trigonal aperture, the sculpture of axial ribs crossed by prominent spiral cords, forming compressed nodules, and the outer lip by having only a few but larger teeth.

Acrista nana (Hervier, 1896) n. comb.

Plate 5, fig. 59

Glyphostoma comptum var. *nana* Hervier, 1896a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: The freshly collected specimen in this study has brownish-orange colored grooves between the intersection of the spiral cords and faintly between the ribs, features absent in the type material. It is assumed that the type species are specimens that lost the coloration since all other morphological characters agree well.
Even though *Pleurotoma compta* Reeve, 1845 is a typical *Lienadia*, the present subspecies is more indicative of *Acrista* as defined herein.
This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes, but was described from the Loyalty Island, therefore is not new to New Caledonia.

Acrista latirella (Melvill & Standen, 1896) n. comb.

Plate 5, fig. 57

Mangilia (*Glyphostoma*) *latirella* Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp8.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes, but was described from Loyalty Island, therefore is not new to New Caledonia.

Acrista pusilla (Dunker, 1871) n. comb.

Plate 5, fig. 56

Clathurella pusilla G. Dunker, 1871.

Type locality: Viti Islands [Fiji].

Material examined: New Caledonia, Ile des Pins: st. idp2, idp3, idp4, idp5, idp6, idp7.

Remarks: is very similar to *Glyphostoma trigonostomum* Hervier, 1896b

Acrista tuberculifera (Hervier, 1896) n. comb.

Plate 5, fig. 58

Glyphostoma marchei var. *tuberculifera* Hervier, 1896a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp3.2.

Remarks: Our single specimen agrees well with the type specimen of *Glyphostoma marchei* var. *tuberculifera* Hervier, 1896 (syntype MNHN-IM-2000-30091). However, we have strong doubts about the validity of the presumed type specimens since they are not even remotely simililar to the type of *Lienardia marchei* Jousseaume, 1884 (syntype MNHN-IM-2000-3082). Given that the existent types of *Glyphostoma marchei* var. *tuberculifera* are instead much closer to *Glyphostoma disconica* Hervier (1896) (syntype MNHN-IM-2000-2904), described in the same publication, is a further hint of a possible confusion of the type specimens. Unfortunately, an original figure of the *Glyphostoma marchei* var. *tuberculifera* type is missing and the meagreness of the orginal description is of little help. However, the resolving this dilemma is beyond the scope of the present paper but could be of interest to future workers.

Genus *Clathurella* Carpenter, 1857

Type species: *Clavatula rava* Hinds, 1843 accepted as *Clathurella rava* (Hinds, 1843) (type by subsequent designation). Type locality: 18 fm [33 m], Gulf of Nicoya, Central America.

Clathurella verrucosa Stahlschmidt, Poppe & Tagaro, 2018

Plate 5, fig. 63

Clathurella verrucosa Stahlschmidt, Poppe & Tagaro, 2018.

Type locality: Pamilacan Island, Bohol, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp7.

Genus *Etrema* Hedley, 1918

Type species: *Mangilia* (*Glyphostoma*) *aliciae* Melvill & Standen, 1895 accepted as *Etrema aliciae* (Melvill & Standen, 1895) (type by original designation). Type locality: Lifou, New Caledonia.

Etrema cf. *crassilabrum* (Reeve, 1843)

Plate 6, fig. 76

Pleurotoma crassilabrum Reeve, 1843.

Type locality: Ticao Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp1.

Remarks: The present species is very similar to *Etrema crassilabrum* (Reeve, 1843) but differs slightly in the weaker spiral sculpture and the less developed denticles in the columella. However, the single available specimen is subadult and a comparison of adult specimens with the type or topotypic specimens is required to provide confirmation.

Etrema aff. *crassilabrum* (Reeve, 1843)

Plate 6, fig. 75

Material examined: New Caledonia, Ile des Pins: st. idp3.2.

Remarks: The present species differs from *Etrema crassilabrum* (Reeve, 1843) in the denser and weaker axial sculpture as well as in a different colouration.

Etrema cf. *glabriplicatum* (Sowerby III, 1913)

Plate 6, fig. 77

Glyphostoma glabriplicatum G. B. Sowerby III, 1913.

Type locality: Osumi, Japan.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp4.

Remarks: The present species is similar to *Etrema glabriplicatum* (Sowerby III, 1913) but differs in the stouter profile, brown coloration below periphery on later teleoconch whorls and the denser axial sculpture.

Etrema cf. *polydesma* Hedley, 1922

Plate 6, fig. 73

Etrema polydesma Hedley, 1922.

Type locality: 15 fm. [27 m], Palm Islands, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3.2, idp5.2, idp8.

Remarks: The present species appears to be conspecific with *Etrema polydesma* Hedley, 1922, but differs slightly in the colouration and sculpture. A comparison with the type or fresh topotypic specimens is required to provide confirmation.

Etrema sp. 1a

Plate 6, fig. 70

Material examined: New Caledonia, Ile des Pins: st. idp2, idp3.2, idp5.2, idp7.

Remarks: The present species is remotely related to *Etrema polydesma* Hedley, 1922, but differs in the less angulated whorls.

Etrema sp. 1b

Plate 6, fig. 71

Material examined: New Caledonia, Ile des Pins: st. idp1.

Remarks: The present species might be conspecific with *Etrema* sp.1 but differs slightly in the colouration and sculpture. More specimens are required to examine if the differences are stable or just within the intraspecific variation.

Etrema sp. 1c

Plate 6, fig. 72

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: The present species is also similar to *Etrema* sp.1 but differs in the more angulated whorls and the rougher axial and spiral sculpture.

Etrema sp. 5

Plate 6, fig. 78

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: The present species is only known by a single subadult specimens, but differs in sculpture and colour pattern from all other species reported here.

Etrema sp. 6

Plate 6, fig. 74

Material examined: New Caledonia, Ile des Pins: st. idp4.

Remarks: The present species is known from one subadult specimen and is remotely similar to *Etrema crassilabrum* but differs in the less angulated whorls and different colour pattern.

Genus *Lienardia* Jousseaume, 1883

Type species: *Clavatula rubida* Hinds, 1843 accepted as *Lienardia rubida* (Hinds, 1843) (type by original designation).Type locality: 7 fm [13 m], New Guinea.

Lienardia compta (Reeve, 1845)

Plate 5, fig. 60

Pleurotoma compta Reeve, 1845.

Type locality: Baclayon, Bohol Island, Philippines.

Material examined: New Caledonia, Ile des Pins: idp3, idp3.2, idp5, idp5.2, idp6, idp7.

Lienardia fallax (G. Nevill & H. Nevill, 1875)

Plate 6, fig. 64

Clathurella rugosa var. *fallax* G. & H. Nevill, 1875.

Type locality: Mauritius and Bourbon [Reunion]; Ceylon [Sri Lanka].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp7, idp8.

Lienardia giliberti (Souverbie in Souverbie & Montrouzier, 1874)

Plate 6, fig. 67

Pleurotoma giliberti Souverbie in Souverbie & Montrouzier, 1874.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp4, idp7.

Lienardia mighelsi Iredale & Tomlin, 1917

Plate 6, fig. 66

Lienardia mighelsi Iredale & Tomlin, 1917.

Type locality: Sandwich Islands [Hawaii].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7.

Lienardia roseotincta (Montrouzier in Souverbie & Montrouzier, 1872)

Plate 6, fig. 68

Pleurotoma (*Clathurella*) *roseotincta* Montrouzier in Souverbie & Montrouzier, 1872.

Type locality: Art Island, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp3.2, idp4, idp5, idp5.2.

Lienardia tricolor (Brazier, 1876)

Plate 6, fig. 65

Clathurella tricolor Brazier, 1876.

Type locality: Palm Island, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp5, idp6.

Lienardia aff. *vultuosa* (Reeve, 1845)

Plate 6, fig. 69

Pleurotoma vultuosa Reeve, 1845.

Type locality: Baclayon, Bohol Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp4.

Remarks: The present morphotype is similar to *Lienardia vultuosa* (Reeve, 1845) but differs in having a stouter shell profile and fewer denticles in the interior of the outer lip. The specimens analysed here appear to belong to the *Lienardia vultuosa-leucostigmata-rhodacme* species-complex. A detailed study is needed to establish limits of either interspecific or intraspecific variation based on coloration, sculpture and lip dentation.

Lienardia sp. 1

Plate 5, fig. 61

Material examined: New Caledonia, Ile des Pins: st. idp1, idp6.

Remarks: Specimens collected and analysed in this study were not recorded in the MNHN unpublished catalogue of morphotypes.

Lienardia sp. 2

Plate 5, fig. 62

Material examined: New Caledonia, Ile des Pins: st. idp3.2.

Remarks: This morphotype was not recorded in the MNHN catalogue of morphotypes.

Genus *Nannodiella* Dall, 1919

Type species: *Philbertia* (*Nannodiella*) *nana* Dall, 1919 accepted as *Nannodiella nana* (Dall, 1919) (type by original designation). Type locality: 26 fm [48 m], off Cacachitas, Gulf of California.

Remarks: The following two species are only provisionally placed in *Nannodiella* due to the similar shell shapes and the spout-like anal sinus, characters that may prove to be artificial. The type species of the

genus *Nannodiella*, *Philbertia* (*Nannodiella*) *nana* Dall 1919, an east pacific species, lacks the apertural denticles which are well developed in *N. acricula* and *N.* cf. *tortilabia.*

Nannodiella acricula (Hedley, 1922)

Plate 5, fig. 54

Etrema acricula Hedley, 1922.

Type locality: 5-8 fm. [9-15 m], Murray Island, Queensland, Australia.

Material examined: New Caledonia, Isle des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp7, idp8.

Nannodiella cf. *tortilabia* (Hedley, 1922)

Plate 5, fig. 55

Etrema tortilabia Hedley, 1922.

Type locality: 5-8 fm. [9-15 m], off Murray Island, Queensland, Australia.

Material examined: New Caledonia, Isle des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Remarks: The present morphotype appears to be *Nannodiella tortilabia* (Hedley, 1922). However, the type of the latter species is of poor quality and the figure by Hedley (1922) only illustrated a specimen with a much more acute apex, further complicating the identification of the morphotype. Verification of specimens from the type locality, or nearby, is necessary to confirm the true identity of this specimen.

Family Raphitomidae Bellardi, 1875

76 morphotypes.

Genus *Austrodaphnella* Laseron, 1954

Type species: *Austrodaphnella clathrata* Laseron, 1954 (type by original designation). Type locality: Pittwater, NSW, Australia.

Austrodaphnella torresensis Shuto, 1983

Plate 11, fig. 140

Austrodaphnella torresensis Shuto, 1983.

Type locality: 9-15 m, off Murray Islands, Torres Strait, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp5, idp5.2, idp6, idp7, idp8.

Genus *Daphnella* Hinds, 1844

Type species: *Pleurotoma lymneiformis* Kiener, 1839 accepted as *Daphnella lymneiformis* (Kiener, 1839) (type by subsequent designation). Type locality: Mauritius.

Daphnella canaliculata Ardovini, 2009

Plate 11, fig. 145

Daphnella canaliculata Ardovini, 2009.

Type locality: 100 m, off Balicasag Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp7.

Daphnella ornata Hinds, 1844

Plate 11, fig. 143

Daphnella ornata Hinds, 1844.

Type locality: 6 fm [11 m], in mud, New Guinea.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp6, idp7.

Daphnella pluricarinata (Reeve, 1845)

Plate 11, fig. 141

Pleurotoma pluricarinata Reeve, 1845.

Type locality: 7 fm [13 m], Burias Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp5.

Remarks: *Daphnella atractoides* Hervier, 1897 is a synonym of *Daphnella pluricarinata* (Reeve, 1845).

Daphnella vitrea Garrett, 1873

Plate 10, fig. 136

Daphnella vitrea Garrett, 1873.

Type locality: Paumotus Isles [Tuamotu, French Polynesia].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3.

Daphnella sp. 2

Plate 11, fig. 146

Material examined: New Caledonia, Ile des Pins: st. idp4, idp5.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

***Daphnella* sp. 3**
Plate 10, fig. 135

Material examined: New Caledonia, Ile des Pins: st. idp8.

Genus *Diaugasma* Melvill, 1917

Type species: *Daphnella epicharta* Melvill & Standen, 1903 accepted as *Diaugasma epicharta* (Melvill & Standen, 1903) (type by monotypy). Type locality: 24°58'N, 56°54'E; 156 fathoms [285 m], Gulf of Oman.

***Diaugasma olyra* (Reeve, 1845)**
Plate 11, fig. 144

Pleurotoma olyra Reeve, 1845.

Type locality: Unknown.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp5, idp6, idp7, idp8.

Genus *Eucyclotoma* Boettger, 1895

Type species: *Clathurella bicarinata* Pease, 1863 accepted as *Eucyclotoma bicarinata* (Pease, 1863) (type by subsequent designation). Type locality: Kingsmill Islands, Kiribati.

***Eucyclotoma bicarinata* (Pease, 1863)**
Plate 10, fig. 138

Clathurella bicarinata Pease, 1863.

Type locality: Kingsmill Islands, Kiribati.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp5, idp6.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

***Eucyclotoma carinulata* (Souverbie, 1875)**
Plate 11, fig. 139

Pleurotoma carinulata Souverbie, 1875.

Type locality: Art Island, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp7.

***Eucyclotoma* cf. *tricarinata* (Kiener, 1839)**
Plate 10, fig. 137

Pleurotoma tricarinata Kiener, 1839.

Type locality: Unknown.

Material examined: New Caledonia, Ile des Pins: st. idp7.

Genus *Exomilus* Hedley, 1918

Type species: *Mangelia lutaria* Hedley, 1907 accepted as *Exomilus lutarius* (Hedley, 1907) (type by original designation). Type locality: 80 fm. [146 m], 22 miles E of Narrabeen, NSW, Australia.

Remarks: We follow Fedosov & Puillandre (2012) by using the genus *Exomilus* for the following two species, even though the type of *Exomilus* is a temperate species and probably not related to the species listed here, while some of the species currently placed in *Kermia* or *Pseudodaphnella* appear to be closer. However, the delimitation of these complicated genera needs molecular methods and is beyond the scope of the present paper. The use of *Exomilus* is utilized for the reason of consistency.

***Exomilus compressus* Fedosov & Puillandre, 2012**
Plate 8, fig. 99

Exomilus compressa Fedosov & Puillandre, 2012.

Type locality: 15°24'22"S, 167°13'02"E, 38 m, Palikulo Bay, Vanuatu.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp4, idp5, idp5.2, idp6, idp7, idp8.

***Exomilus edychrous* (Hervier, 1897)**
Plate 8, fig. 101

Clathurella edychroa Hervier, 1897a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Genus *Hemilienardia* O. Boettger, 1895

Type species: *Pleurotoma* (*Defrancia*) *malleti* Récluz, 1852 accepted as *Hemilienardia malleti* (Récluz, 1852) (type by original designation). Type locality: Pacific Ocean.

***Hemilienardia acinonyx* Fedosov *et al.*, 2017**
Plate 7, fig. 85

Hemilienardia acinonyx Fedosov, Stahlschmidt, Puillandre, Aznar-Cormano & Bouchet, 2017.

Type locality: Panglao Island, off Momo Beach, lumun-lumun net, 60-80 m.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp5, idp5.2, idp8.

***Hemilienardia calcicincta* (Melvill & Standen, 1895)**
Plate 7, fig. 83

Mangilia (Glyphostoma) calcicincta Melvill & Standen, 1895.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp2.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes, but was described from Lifou, therefore is not new to New Caledonia.

***Hemilienardia* cf. *gemmulata* Wiedrick, 2017**
Plate 7, fig. 82

Hemilienardia gemmulata Wiedrick, 2017.

Type locality: 11°29'0.12"N, 119°50'13.82"E; in tangle nets at 150 m, off Linapacan Island, Palawan Province, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp5.2.

Remarks: There is a group of very similar species, morphologically comprising of *Hemilienardia gemmulata, H. fenestrata* (Melvill, 1898), and *H. hersilia* (Hedley, 1922), that appear to be different species. The present morphotype appears to differ slightly from *Hemilienardia gemmulata* in the larger size, more shouldered whorls, and denser sculpture. Molecular studies are required for a resolution to this species complex.

***Hemilienardia homochroa* Hedley, 1922**
Plate 7, fig. 79

Hemilienardia homochroa Hedley, 1922.

Type locality: Two Isles, off Cape Flattery, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp1.

***Hemilienardia idiomorpha* (Hervier, 1897) n. comb.**
Plate 7, fig. 84

Clathurella idiomorpha Hervier, 1897a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1.

Remarks: The diagonally cancellated protoconch is indicative of the family Raphitomidae and this species is tentatively assigned to the genus *Hemilienardia*.

***Hemilienardia malleti* (Récluz, 1852)**
Plate 7, fig. 80

Pleurotoma (Defrancia) malleti Récluz, 1852.

Type locality: Pacific Ocean.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3.2, idp4, idp5, idp6, idp7.

***Hemilienardia mikesevernsi* Wiedrick, 2017**
Plate 7, fig. 81

Hemilienardia mikesevernsi Wiedrick, 2017.

Type locality: 19°40'3.18"N, 156°1'48.91"W; in sand and rubble at 8-29 m, Off Honokohau Harbor, Kona North District, Hawai'i, Hawaiian Islands.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3.2.

***Hemilienardia shawnmilleri* Wiedrick, 2017**
Plate 7, fig. 87

Hemilienardia shawnmilleri Wiedrick, 2017.

Type Locality: 26°50.8'N, 128°17.2'E; in sand and coral among channels and caves at 12-20 m, North northwest Oku, Ryukyushoto, Okinawa-jima, Okinawa Prefecture, Japan.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3.2, idp5.2, idp6.

***Hemilienardia* sp.**
Plate 7, fig. 86

Material examined: New Caledonia, Ile des Pins: st. idp1, idp5, idp5.2.

Genus *Kermia* W. R. B. Oliver, 1915

Type species: *Kermia benhami* W. R. B. Oliver, 1915. (type by original designation). Type locality: 10-30 m, near Sunday Island, Kermadec Islands.

***Kermia benhami* Oliver, 1915**
Plate 8, fig. 102

Kermia benhami Oliver, 1915.

Type locality: 10-30 m, near Sunday Island, Kermadec Islands.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp7, idp8.

Kermia cf. *benhami* Oliver, 1915

Plate 8, fig. 103

Material examined: New Caledonia, Ile des Pins: st. idp5, idp6.

Remarks: The New Caledonian morphotype is similar to *Kermia benhami* (Oliver, 1915), but differs in broader and more angulate whorls, as well as in a different ratio of aperture length to total shell length, (1.9 versus 2.3 for *K. benhami*). The specimens sampled from southern New Caledonia were not recorded in the unpublished MNHN catalogue of morphotypes.

Kermia episema (Melvill & Standen, 1896)

Plate 9, fig. 117

Clathurella episema Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp7, idp8.

Kermia melanoxytum (Hervier, 1896)

Plate 9, fig. 122

Glyphostoma melanoxytum Hervier, 1896a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Kermia sp.20

Plate 8, figs 104-106

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp7, idp8.

Remarks: These morphotypes may prove to be a species complex, as they vary in pattern, shape, and colour. But since all kind of intermediates exist, it is difficult to draw a line and segregate them into morphospecies. Molecular studies are required for resolving this species complex.

Genus *Kuroshiodaphne* Shuto, 1965

Type species: *Daphnella fuscobalteata* E. A. Smith, 1879 accepted as *Kuroshiodaphne fuscobalteata* (E. A. Smith, 1879) (type by original designation). Type locality: Station 21.33°45'N, 132°30'E; 30 fathoms [55 m], between south-western extremity of Niphon and the island of Shikoku [Japan].

Kuroshiodaphne aff. *supracancellata* (Schepman, 1913)

Plate 11, fig. 142

Daphnella supracancellata Schepman, 1913.

Type locality: 75 m, Kwandang Bay entrance. [Sulawesi, Indonesia].

Material examined: New Caledonia, Ile des Pins: st. idp5.

Remarks: The specimen collected is similar to *Kuroshiodaphne supracancellata* (Schepman, 1913), but differs in the less convex whorls, broader spiral cords, and the less constricted aperture at the anterior and posterior ends. This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Genus *Microdaphne* McLean, 1971

Type species: *Philbertia trichodes* Dall, 1919 accepted as *Microdaphne trichodes* (Dall, 1919) (type by original designation). Type locality: Panama Bay.

Microdaphne morrisoni Rehder, 1980

Plate 11, fig. 153

Microdaphne morrisoni Rehder, 1980.

Type locality: Moto Mataira, Raoia, Tuamotu Islands [French Polynesia].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Genus *Pleurotomella* Verrill, 1872

Type species: *Pleurotomella packardii* Verrill, 1872. (type by monotypy). Type locality: 42°11'N, 67°17'W; 150 fm [275 m], St. George's Bank.

Pleurotomella cf. *itama* (Melvill, 1906)

Plate 12, fig. 156

Daphnella (*Pleurotomella*) *itama* Melvill, 1906.

Type locality: 24°58'N, 56°54'E; 156 fm [285 m], Gulf of Oman.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3.

Remarks: The generic placement of that species is tentative. The specimens collected seem to be

congeneric to *Pleurotomella itama* (Melvill, 1906) described from the Gulf of Oman, but differ from the latter by the stronger sculpture and the more angulated whorls.

Genus *Pseudodaphnella* Boettger, 1895

Type species: *Pleurotoma philippinensis* Reeve, 1843 accepted as *Pseudodaphnella philippinensis* (Reeve, 1843) (type by original designation). Type locality: found under stones at low water, Islands of Masbate and Luzon, Philippines.

Pseudodaphnella cf. *apicalis* (Montrouzier in Souverbie, 1861)

Plate 10, fig. 127

Pleurotoma apicalis Montrouzier in Souverbie, 1861.

Type locality: Art Island, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp8.

Remarks: The present specimen might be *Pseudodaphnella apicalis* (Montrouzier, 1861), but differs in having more shouldered whorls.

Pseudodaphnella aureotincta (Hervier, 1897)

Plate 9, fig. 112

Clathurella tincta var. *aureotincta* Hervier, 1897a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp5.2.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes, but was described from Lifou, and therefore is not new to New Caledonia.

Pseudodaphnella cf. *barnardi* (Brazier, 1876)

Plate 9, fig. 110

Clathurella barnardi Brazier, 1876.

Type locality: Barnard Island, north east Australia [Queensland].

Material examined: New Caledonia, Ile des Pins: st. idp2.

Remarks: According to Fedosov & Puillandre, 2012, "*Pseudodaphnella phaeogranulata* nov. sp. strongly resembles *P. barnardi*, its closest molecular relative. The only difference seems to be in the colour of the axial bands, which are black in *P. barnardi* and brown in *P. phaeogranulata*." The coloration of the present species is blackish-brown and without molecular confirmation, its identity is uncertain.

Pseudodaphnella caelata (Garrett, 1873)

Plate 9, fig. 123

Clathurella caelata, Garrett, 1873.

Type locality: Viti Isles [Fiji].

Material examined: New Caledonia, Ile des Pins: st. idp2.

Pseudodaphnella caletria (Melvill & Standen, 1896)

Plate 8, fig. 94

Clathurella caletria Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2.

Pseudodaphnella daedalea (Garrett, 1873)

Plate 10, fig. 126

Clathurella daedalea Garrett, 1873.

Type locality: Viti Isles [Fiji].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp5, idp6, idp7.

Pseudodaphnella aff. *drupelloides* (Kilburn, 2009)

Plate 8, fig. 108

Kermia drupelloides Kilburn, 2009.

Type locality: 30°17′S, 30°45′E; ca -35 m, in shell grit, off Scottburgh, KwaZulu-Natal, South Africa.

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: The New Caledonian morphotype is very similar to *Pseudodaphnella drupelloides* (Kilburn, 2009) but appears to differ in having slightly stronger knobs on the teleoconch whorls and a stronger parietal pad that constricts the opening of the anal sinus.

Pseudodaphnella fallax Fedosov & Puillandre, 2012

Plate 9, fig. 113

Pseudodaphnella fallax Fedosov & Puillandre, 2012.

Type locality: stn. B19, 9°29.4'N, 123°56.0'E; 17 m, Expedition 'Panglao 2004', Pamilacan Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp6.

Pseudodaphnella granosa (Dunker, 1871)
Plate 8, fig. 107

Clathurella granosa G. Dunker, 1871.

Type locality: Upolu [Samoa].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp3.2, idp5, idp5.2, idp6, idp7.

Pseudodaphnella hadfieldi (Melvill & Standen, 1895)
Plate 10, fig. 124

Pleurotoma (*Drillia*) *hadfieldi* Melvill & Standen, 1895.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp7.

Pseudodaphnella infrasulcata (Garrett, 1873)
Plate 8, fig. 98

Clathurella infrasulcata Garrett, 1873.

Type locality: Viti Isles [Fiji].

Material examined: New Caledonia, Ile des Pins: st. idp6, idp7.

Pseudodaphnella aff. *lineata* Fedosov & Puillandre, 2012
Plate 9, fig. 114

Pseudodaphnella lineata Fedosov & Puillandre, 2012.

Type locality: stn. B25, 9°29.4'N, 123°56.1'E; 16 m, Expedition 'Panglao 2004', Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp1.

Remarks: The Ile des Pins specimen differs from typical *Pseudodaphnella lineata* Fedosov & Puillandre, 2012 in having a slightly stronger spiral sculpture and the less-convex and almost flat-sided whorls, resulting in a different shell profile.

Pseudodaphnella martensi (G. Nevill & H. Nevill, 1875)
Plate 9, fig. 115

Clathurella martensi G. Nevill & H. Nevill, 1875.

Type locality: Balapiti in Ceylon [Sri Lanka].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp4, idp6, idp7.

Pseudodaphnella philippinensis (Reeve, 1843)
Plate 10, fig. 129

Pleurotoma philippinensis Reeve, 1843.

Type locality: Masbate and Luzon Islands, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp2.

Pseudodaphnella producta (Pease, 1860)
Plate 10, fig. 125

Clathurella producta Pease, 1860.

Type locality: Sandwich Islands [Hawaii].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp5, idp5.2, idp6, idp7, idp8.

Pseudodaphnella punctifera (Garrett, 1873)
Plate 9, fig. 121

Clathurella punctifera Garrett, 1873.

Type locality: Society, Samoa, and Viti [Fiji].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp5, idp7.

Pseudodaphnella aff. *punctifera* (Garrett, 1873)
Plate 9, fig. 120

Material examined: New Caledonia, Ile des Pins: st. idp7.

Remarks: The Ile des Pins morphotype differs from *Pseudodaphnella punctifera* (Garrett, 1873) in having a stronger sculpture and different coloration.

Pseudodaphnella rubroguttata (H. Adams, 1872)
Plate 9, fig. 118

Clathurella rubro-guttata H. Adams, 1872.

Type locality: New Hebrides [Vanuatu].

Material examined: New Caledonia, Ile des Pins: st. idp1.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Pseudodaphnella cf. *rubroguttata* (Adams, 1872)
Plate 9, fig. 119

Material examined: New Caledonia, Ile des Pins: st. idp1, idp5.2.

Remarks: Specimens from New Caledonia are similar to *Pseudodaphnella rubroguttata* (Adams, 1872) but

have a less bulbous outline and a stronger parietal region that constricts the opening of the anal sinus.

***Pseudodaphnella santoa* Fedosov & Puillandre, 2012**
Plate 9, fig. 116

Pseudodaphnella santoa Fedosov & Puillandre, 2012.

Type locality: 15°32'23"S, 167°12'08"E; Aoré Is., N Side of Ambuei Bay, Vanuatu.

Material examined: New Caledonia, Ile des Pins: st. idp1.

***Pseudodaphnella spyridula* (Melvill & Standen, 1896)**
Plate 8, fig. 100

Clathurella spyridula Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3.2, idp4, idp5, idp5.2, idp7.

***Pseudodaphnella thereganum* (Melvill & Standen, 1896)**
Plate 7, fig. 89

Mangilia (*Glyphostoma*) *thereganum* Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp5.2, idp7.

***Pseudodaphnella thespesia* (Melvill & Standen, 1896)**
Plate 10, fig. 128

Daphnella thespesia Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp5, idp8.

***Pseudodaphnella tigroidella* (Hervier, 1896)**
Plate 7, fig. 93

Glyphostoma tigroidellum Hervier, 1896a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp3.2, idp4, idp5, idp6, idp7, idp8.

***Pseudodaphnella* cf. *tincta* (Reeve, 1846)**
Plate 9, fig. 111

Pleurotoma tincta Reeve, 1846.

Type locality: Unknown.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp3, idp3.2, idp4, idp5, idp6, idp7.

Remarks: The present morphotype is similar to *Pseudodaphnella tincta* (Reeve, 1846) but differs in the stronger sculpture, the larger size and lower number of apertural denticles and coloration.

***Pseudodaphnella* sp. 8**
Plate 7, fig. 92

Material examined: New Caledonia, Ile des Pins: st. idp2, idp3, idp3.2, idp5, idp6, idp7.

***Pseudodaphnella* sp. 9**
Plate 8, fig. 96

Material examined: New Caledonia, Ile des Pins: st. idp3, idp5.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

***Pseudodaphnella* sp. 10**
Plate 7, fig. 88

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp5, idp6.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

***Pseudodaphnella* sp. 11**
Plate 8, fig. 95

Material examined: New Caledonia, Ile des Pins: st. idp2.

***Pseudodaphnella* sp. 12**
Plate 7, fig. 90

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

***Pseudodaphnella* sp. 14**
Plate 8, fig. 97

Material examined: New Caledonia, Ile des Pins: st. idp3, idp5.

Pseudodaphnella sp. 15
Plate 7, fig. 91

Material examined: New Caledonia, Ile des Pins: st. idp1, idp5.

Pseudodaphnella sp. 21
Plate 9, fig. 109

Material examined: New Caledonia, Ile des Pins: st. idp6.

Genus *Thetidos* Hedley, 1899

Type species: *Thetidos morsura* Hedley, 1899 (type by original designation). Type locality: 40-80 fm [73-146 m], Funafuti Atoll, [Tuvalu].

Thetidos cf. *morsura* Hedley, 1899
Plate 12, fig. 154

Thetidos morsura Hedley, 1899.

Type locality: 40-80 fm [73-146 m], Funafuti Atoll, [Tuvalu].

Material examined: New Caledonia, Ile des Pins: st. idp3.2, idp5.2.

Remarks: Fedosov & Stahlschmidt (2014) demonstrated that *Thetidos morsura* either displays considerable morphological variability in shell structure and colouration or represents a complex of related species. The present morphospecies is less globular but more pyramidal in shape and has higher aperture. This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Genus *Tritonoturris* Dall, 1924

Type species: *Clathurella robillardi* H. Adams, 1869 accepted as *Tritonoturris amabilis* (Hinds, 1843) (type by original designation). Type locality: Barkly Island, Mauritius.

Tritonoturris cumingii (Powys, 1835)
Plate 10, fig. 130

Buccinum cumingii Powys in Powys & G. B. Sowerby I, 1835.

Type locality: Grimwood's Isle [Fangatau southeast of Mururoa, Tuamotu Archipelago, French Polynesia].

Material examined: New Caledonia, Ile des Pins: st. idp2, idp5.

Tritonoturris lifouana (Hervier, 1897)
Plate 10, fig. 134

Daphnella lifouana Hervier, 1897a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp6, idp8.

Tritonoturris menecharmes (Melvill, 1923)
Plate 11, fig. 147

Veprecula menecharmes Melvill, 1923.

Type locality: Mauritius.

Material examined: New Caledonia, Ile des Pins: st. idp3, idp5, idp5.2.

Tritonoturris subrissoides (Hervier, 1897)
Plate 10, fig. 133

Daphnella varicosa var. *subrissoides* Hervier, 1897a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp2, idp3.2, idp5, idp6, idp8.

Tritonoturris cf. *subrissoides* (Hervier, 1897)
Plate 10, fig. 132

Material examined: New Caledonia, Ile des Pins: st. idp5.

Remarks: This morphospecies differs from *Tritonoturris subrissoides* (Hervier, 1897) in having a stronger and denser axial sculpture. Compared to *Tritonoturris* sp. 1, it has less angulate whorls and less recurved axial ribs. This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Tritonoturris sp. 1
Plate 10, fig. 131

Material examined: New Caledonia, Ile des Pins: st. idp6.

Genus *Veprecula* Melvill, 1917

Type species: *Clathurella sykesii* Melvill & Standen, 1903 accepted as *Veprecula sykesii* (Melvill & Standen, 1903) (type by original designation). Type locality: 24°58'N, 56°51' E; 156 fathoms [285 m], Gulf of Oman.

Veprecula aff. *spanionema* (Melvill, 1917)
Plate 11, fig. 148

Clathurina spanionema Melvill, 1917.

Type locality: 24°58'N, 56°51'E; 156 fathoms [285 m], Gulf of Oman.

Material examined: New Caledonia, Ile des Pins: st. idp1.

Remarks: *Veprecula spanionema* (Melvill, 1917) was described from the Gulf of Oman and is only here tentatively recorded, based on an eroded type specimen from idp1. A comparison of fresh material from the type locality is needed to confidently authenticate these two morphotypes as being conspecific.

Veprecula vacillata Hedley, 1922
Plate 11, fig. 149

Veprecula vacillata Hedley, 1922.

Type locality: 5-10 fm [9-18 m], Hope Island, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp4.

Veprecula aff. *vepratica* (Hedley, 1903)
Plate 11, fig. 151

Pleurotoma vepratica Hedley, 1903.

Type localities: 63-75 fm [115-137 m], off Port Kembla; 50-52 fm [91-95 m], off Botany Bay; 41-50 fm [75-91 m], off Cape Three Points; 24 fm [44 m], off Cabbage Tree Island, Port Stephens; Torres Straits.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp4.

Remarks: This morphotype is very similar to *Veprecula vepratica* (Hedley, 1903) but differs in having a higher and has less convex protoconch, as well as fainter sculpture in the teleoconch whorls.

Veprecula sp. 1
Plate 11, fig. 152

Material examined: New Caledonia, Ile des Pins: st. idp1.

Veprecula sp. 2
Plate 11, fig. 150

Material examined: New Caledonia, Ile des Pins: st. idp5.

Raphitomid sp.
Plate 12, fig. 155

Material examined: New Caledonia, Ile des Pins: st. idp3.

Remarks: Unequivocal shell characteristics which would enable an assignment of this species to a genus are missing and, therefore, we assign it tentatively to Incertae sedis rather than to a specific genus.

Family Mangeliidae Fischer, 1883

21 morphotypes

Genus *Eucithara* Fischer, 1883

Type species: *Mangelia stromboides* Reeve, 1846 accepted as *Eucithara stromboides* (Reeve, 1846) (type by original designation). Type locality: Bohol Island, Philippines.

Eucithara celebensis (Hinds, 1843)
Plate 12, fig. 160

Mangelia celebensis Hinds, 1843.

Type locality: 10 fm [18 m], Straits of Macassar.

Material examined: New Caledonia, Ile des Pins: st. idp2.

Eucithara crystallina (Hervier, 1897)
Plate 12, figs 161-162

Cithara crystallina Hervier, 1897b.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp5.

Eucithara cf. *harpellina* (Hervier, 1897)
Plate 12, fig. 157

Cithara harpellina Hervier, 1897b.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: idp2.

Remarks: The present morphotype is similar to *Eucithara harpellina* (Hervier, 1897), but differs in having more shouldered whorls and a finer spiral sculpture.

Eucithara cf. *isseli* (G. Nevill & H. Nevill, 1875)

Plate 12, fig. 159

Cythara isseli G. & H. Nevill, 1875.

Type locality: Balapiti, Ceylon [Sri Lanka].

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp5.2.

Remarks: Compared to typical *Eucithara isseli* (Nevill & Nevill, 1875) specimens, the present specimens differ in having a denser axial sculpture.

Eucithara cf. *lepidella* (Hervier, 1897)

Plate 12, fig. 158

Cithara lepidella Hervier, 1897b.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp3, idp5, idp6.

Remarks: As the type material could not be located, it was not possibly to compare it directly with our specimens. According to the original figure of *E. lepidella*, this form differs in having a denser axial sculpture and more numerous denticles on the inner and outer lips.

Eucithara souverbiei (Tryon, 1884)

Plate 12, fig. 163

Mangilia (*Cythara*) *souverbiei* Tryon, 1884.

Type locality: New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp5, idp8.

Genus *Gingicithara* Kilburn, 1992

Type species: *Mangelia lyrica* Reeve, 1846 accepted as *Gingicithara lyrica* (Reeve, 1846) (type by original designation). Type locality: among coarse sand, 7 fathoms [13 m], Burias Island, Philippines.

Gingicithara notabilis (E. A. Smith, 1888)

Plate 12, figs 164-165

Pleurotoma (*Mangilia*) *notabilis* E. A. Smith, 1888.

Type locality: unknown.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Genus *Heterocithara* Hedley, 1922

Type species: *Clathurella bilineata* Angas, 1871 accepted as *Heterocithara bilineata* (Angas, 1871) (type by original designation). Type locality: Dredge near "Sow and Pigs reef", Port Jackson, NSW, Australia.

Heterocithara diatula (Hervier, 1897) n. comb.

Plate 13, fig. 175

Mangilia diatula Hervier, 1897b.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp4, idp5, idp5.2, idp7.

Heterocithara himerta (Melvill & Standen, 1896)

Plate 13, fig. 168

Mangilia himerta Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp6, idp7, idp8.

Heterocithara isophanes (Hervier, 1897) n. comb.

Plate 13, figs 172-173

Mangilia isophanes Hervier, 1897b.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp5, idp5.2, idp6, idp8.

Remarks: No syntypes of *M. isophanes* were detected at MNHN, but a specimen in the Dautzenberg collection (ISBN; probably received from Hervier) agrees well with the original drawing and with the present specimens. The species shows some variability in the colour pattern of the shell.

Heterocithara strombillum (Hervier, 1896)

Plate 13, fig. 167

Glyphostoma strombillum Hervier, 1896a.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp7, idp8.

Heterocithara sp. 13

Plate 12, fig. 166

Material examined: New Caledonia, Ile des Pins: st. idp5, idp5.2.

Heterocithara sp. 14
Plate 13, fig. 169

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp4, idp5, idp5.2, idp6, idp8.

Heterocithara sp. 16
Plate 13, fig. 170

Material examined: New Caledonia, Ile des Pins: st. idp3, idp5, idp5.2, idp6, idp8.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Heterocithara sp. 17
Plate 13, fig. 171

Material examined: New Caledonia, Ile des Pins: st. idp2, idp5, idp7, idp8.

Heterocithara sp. 18
Plate 13, fig. 174

Material examined: New Caledonia, Ile des Pins: st. idp6.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Heterocithara sp. 19
Plate 13, fig. 176

Material examined: New Caledonia, Ile des Pins: st. idp1, idp2, idp3, idp3.2, idp5, idp5.2, idp7.

Remarks: This morphotype was not recorded in the unpublished MNHN catalogue of morphotypes.

Genus *Macteola* Hedley, 1918

Type species: *Purpura anomala* Angas, 1877 accepted as *Macteola anomala* (Angas, 1877) (type by original designation). Type locality: 25 fathoms [46 m], Port Jackson-Heads, NSW, Australia.

Macteola cf. *interrupta* (Reeve, 1846)
Plate 13, figs 180-181

Mangelia interrupta Reeve, 1846.

Type locality: Ticao Island, Philippines.

Material examined: New Caledonia, Ile des Pins: st. idp1, idp4, idp5.

Remarks: The southern New Caledonian specimens differs from *Macteola interrupta* (Reeve, 1846) by having more sloping whorls resulting in a different shell outline, as well as a completely different colour pattern.

Macteola thalycra (Melvill & Standen, 1896)
Plate 13, fig. 179

Mangilia thalycra; Melvill & Standen, 1896.

Type locality: Lifou, New Caledonia.

Material examined: New Caledonia, Ile des Pins: st. idp5, idp7.

Genus *Pseudorhaphitoma* O. Boettger, 1895

Type species: *Mangelia fairbanki* G. Nevill & H. Nevill, 1875 accepted as *Pseudorhaphitoma fairbanki* (G. Nevill & H. Nevill, 1875) (type by original designation). Type locality: Bombay [India].

Pseudorhaphitoma hervieri Hedley, 1922 n. comb.
Plate 13, fig. 178

Anacithara hervieri Hedley, 1922.

Type locality: 5 to 8 fathoms [9-15 m], Murray Island, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp5, idp7.

Remarks: This species was originally described in the genus *Anacithara* (a genus which is now classified in the Horaiclavidae) but the axially ribbed protoconch is clearly indicative of Mangeliidae. The claviform shells with the high spire, the denticle on the callus of the inner lip, and the granular spiral sculpture is characteristic for the genus *Pseudorhaphitoma* Boettger, 1895.

Pseudorhaphitoma transitans Hedley, 1922
Plate 13, fig. 177

Pseudorhaphitoma transitans Hedley, 1922.

Type locality: 15 fathoms [27 m], Plam Island, Queensland, Australia.

Material examined: New Caledonia, Ile des Pins: st. idp2.

DISCUSSION

While the number of morphotypes observed during this mission seems relatively low compared to the average number of morphospecies reported in the three sites surveyed by the MNHN (approximately 280 species per site), this richness is considered remarkable when taking

into account the limited sampling effort and range of the habitats surveyed. Typical expeditions performed by the MHNH average approximately 500 workdays across all participants for the duration of the mission, compared to a much smaller effort (8 workdays in the field) in the current study. Moreover, only a small portion of the north-western region of Ile des Pins was sampled, with all stations but one within a 4.6 km² proximity. Furthermore, the range of habitats sampled was limited to outer reefs and passages while fringing reefs, intermediate reefs, sea grass beds and other soft bottom habitats where unexplored. In perspective, the area sampled by the Montrouzier expeditions, estimated at 350 km² at Touho and Koumac (Bouchet, 1994), covered a full range of available habitats. Therefore, it is assumed that a comparable sampling effort at Ile des Pins would very likely result in many additional morphotypes.

ACKNOWLEDGMENTS

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Plate 1

Figs 1-12: Drilliidae

(1) *Clavus bilineatus* (Reeve, 1845), 12.6 mm. (2) *Clavus lamberti* (Montrouzier, 1860) 8.2 mm. (3) *Clavus* aff. *lamberti* (Montrouzier, 1860), 6.2 mm. (4) *Clavus virginieae* Kilburn, Fedosov & Kantor, 2014, 9.3 mm. (5) *Clavus formosus* (Reeve, 1846), 14.4 mm. (6) *Iredalea inclinata* (Sowerby III, 1893), 17.0 mm. (7) *Clavus pica* Reeve, 1843, 22.1 mm. (8) *Clavus picoides* Kilburn, Fedosov & Kantor, 2014, 10.9 mm. (9) *Clavus moquinianus* Montrouzier, 1874, 7.4 mm. (10) *Plagiostropha* sp., 5.3 mm. (11) *Iredalea balteata* (Gould, 1860), 4.4 mm. (12) *Iredalea* cf. *balteata* (Gould, 1860), 4.8 mm.

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Plate 2

Figs 13-23: Pseudomelatomidae; Horaiclavidae
(13) *Crassispira scala* Kantor, Stahlschmidt, Aznar-Cormano, Bouchet & Puillandre, 2017, 16.6 mm. (14) *Carinapex philippinensis* Wiedrick, 2015, 3.8 mm. (15) *Carinapex amirowlandae* Wiedrick, 2015, 3.3 mm. (16) *Carinapex minutissima* (Garrett, 1873), 2.5 mm. (17) *Carinapex chaneyi* Wiedrick, 2015, 3.5 mm. (18) *Carinapex mooreorum* Wiedrick, 2015, 2.3 mm. (19) *Ceritoturris theoteles* (Melvill & Standen, 1896) 4.5 mm. (20) *Ceritoturris* cf. *theoteles* (Melvill & Standen, 1896) 4.3 mm. (21) *Ceritoturris papillosa* (Garrett, 1873), 2.6 mm. (22) *Ceritoturris* sp.1, 3.3 mm. (23) *Anacithara* cf. *lita* (Melvill & Standen, 1896) 5.3 mm.

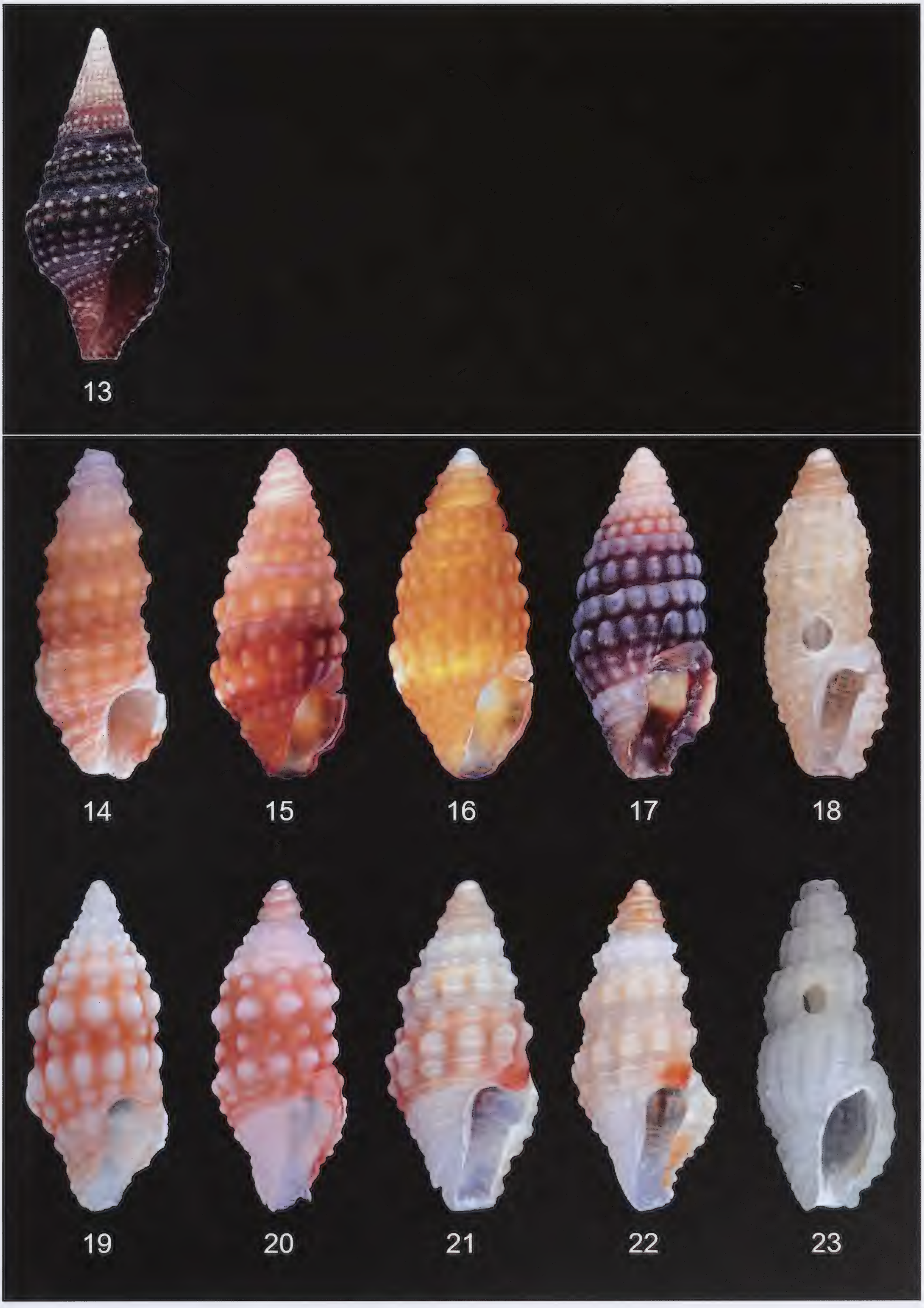
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Plate 3

Figs 24-36: Horaiclavidae; Turridae
(24) *Anacithara* sp.3, 6.4 mm. (25) *Anacithara conata* (Hedley, 1909), 4.6 mm. (26) *Anacithara themeropis* (Melvill & Standen, 1896) 4.3 mm. (27) *Anacithara* cf. *stricta* Hedley, 1922, 4.4 mm. (28) *Graciliclava costata* (Hedley, 1922), 7.3 mm. (29) *Lophiotoma* sp., 33.9 mm. (30) *Turridrupa diffusa* Powell, 1967, 17.5 mm. (31) *Turridrupa* cf. *jubata* (Hinds, 1843), 20.2 mm. (32) *Turridrupa consobrina* Powell, 1967, 13.1 mm. (33) *Turridrupa bijubata* (Reeve, 1843), 13.9 mm. (34) *Xenuroturris millepunctata* (G.B. Sowerby III, 1909), 31.9 mm. (35) *Xenuroturris legitima* Iredale, 1929, 37.0 mm. (36) *Iotyrris cingulifera* (Lamarck, 1822), 28.8 mm.

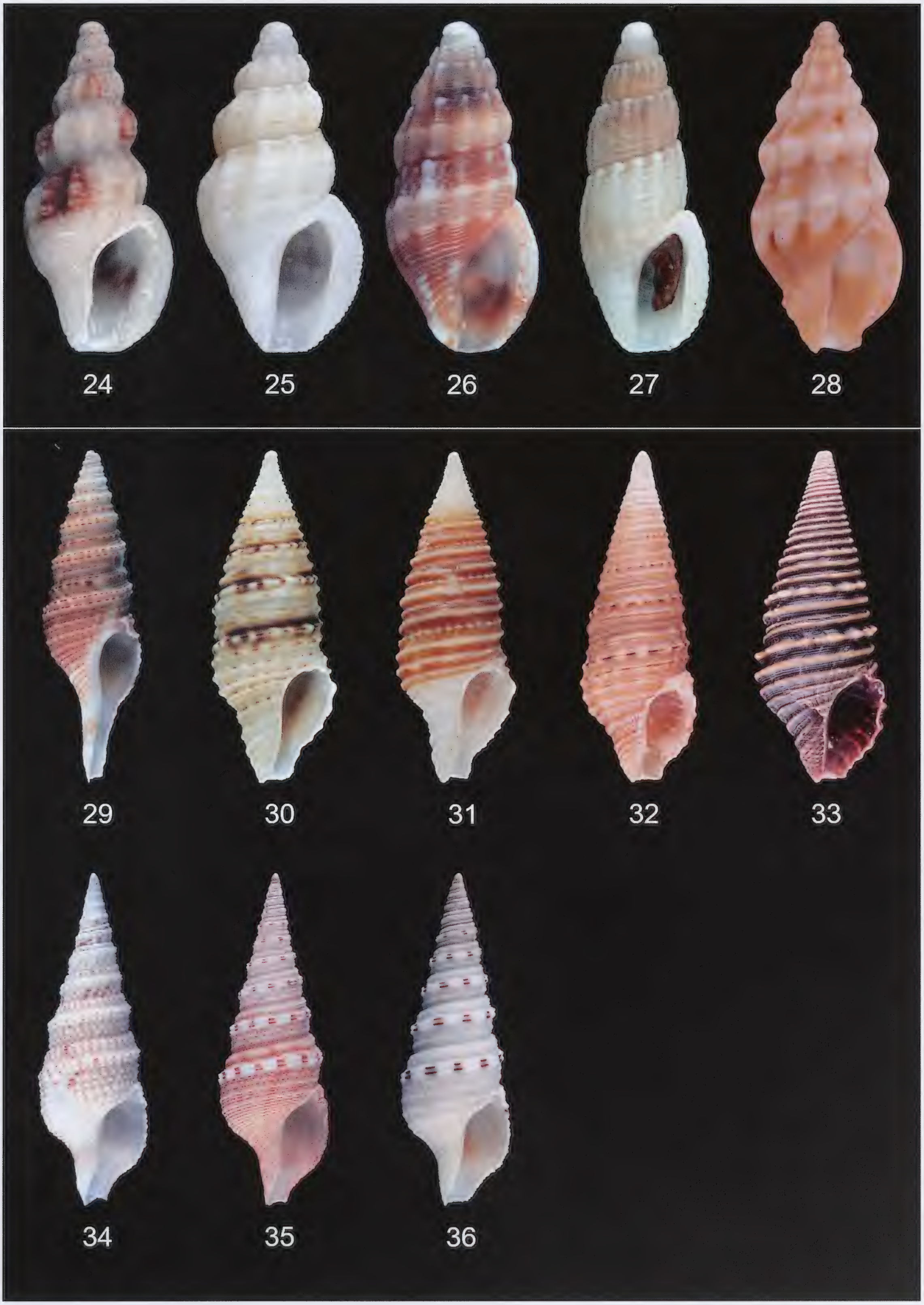
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Plate 4

Figs 37-51: Mitromorphidae. (37) *Lovellona atramentosa* (Reeve, 1849), 9.2 mm. (38) *Mitromorpha* sp.6, 7.3 mm. (39) *Mitromorpha drivasi* Chang, 1995, 6.6 mm. (40) *Mitromorpha fisheri* (Hervier, 1900), 5.2 mm. (41) *Mitromorpha* sp.3 6.4 mm. (42-43) *Mitromorpha metula* (Hinds, 1843), 3.6 mm, 5.3 mm. (44) *Mitromorpha sublachryma* (Hervier, 1900), 6.2 mm. (45) *Mitromorpha* cf. *sublachryma* morph 1 (Hervier, 1900), 6.5 mm. (46) *Mitromorpha* cf. *sublachryma* morph 2 (Hervier, 1900), 9.1 mm. (47) *Mitromorpha* cf. *sublachryma* morph 3 (Hervier, 1900), 4.8 mm. (48) *Mitromorpha inornata* (Hervier, 1900), 4.6 mm. (49) *Mitromorpha* sp. 5, 6.2 mm. (50) *Mitromorpha iozona* (Hervier, 1900), 5.4 mm. (51) *Mitromorpha alphonsiana* (Hervier, 1900), 5.5 mm.

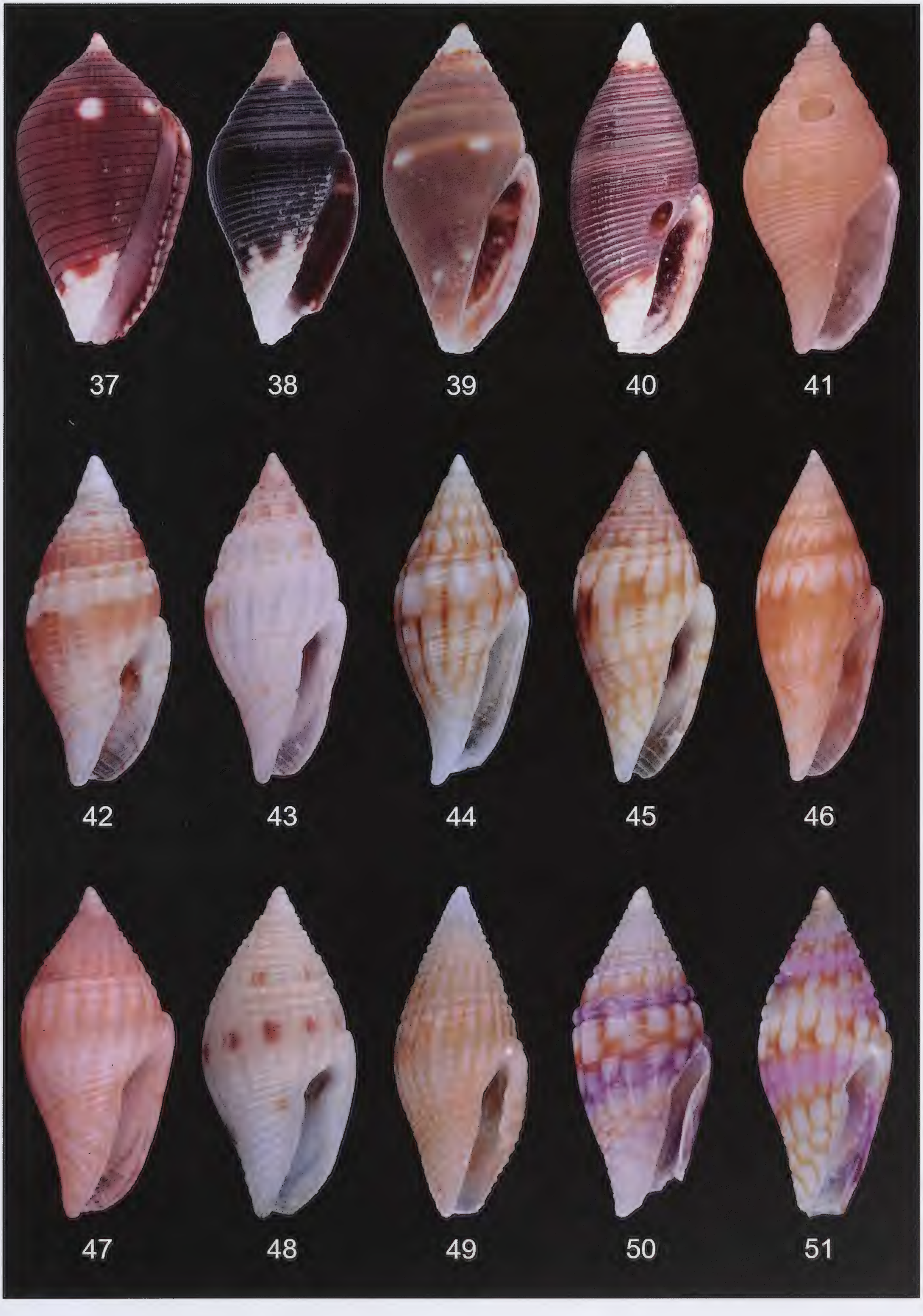
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Plate 5

Figs 52-63: Mitromorphidae; Clathurellidae. (52) *Mitromorpha salisburyi* (Cernohorsky, 1978), 4.3 mm. (53) *Mitromorpha* aff. *thalaoides* (Chino & Stahlschmidt, 2014), 4.7 mm. (54) *Nannodiella acricula* (Hedley, C., 1922), 3.1 mm. (55) *Nannodiella cf. tortilabia* (Hedley, C., 1922), 3.4 mm. (56) *Acrista pusilla* (Dunker, 1871), 4.0 mm. (57) *Acrista latirella* (Melvill, Standen, 1896), 3.5 mm. (58) *Acrista tuberculifera* (Hervier, 1896), 4.8 mm. (59) *Acrista nana* (Hervier, 1896), 6.3 mm. (60) *Lienardia compta* (Reeve, 1845), 7.3 mm. (61) *Lienardia* sp. 1, 8.1 mm. (62) *Lienardia* sp. 2, 4.9 mm. (63) *Clathurella verrucosa* Stahlschmidt, Poppe & Tagaro, 2018, 4.7 mm.

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Plate 6

Figs 64-78: Clathurellidae. (64) *Lienardia fallax* (G. Nevill & H. Nevill, 1875), 4.4 mm. (65) *Lienardia tricolor* (Brazier, 1876), 6.4 mm. (66) *Lienardia mighelsi* Iredale & Tomlin, 1917, 6.3 mm. (67) *Lienardia giliberti* (Souverbie, S.M. in Souverbie, S.M. & R.P. Montrouzier, 1874), 7.4 mm. (68) *Lienardia roseotincta* (Montrouzier in Souverbie & Montrouzier, 1872), 7.7 mm. (69) *Lienardia* aff. *vultuosa* (Reeve, 1845), 10.9 mm. (70) *Etrema* sp. 1, 10.0 mm. (71) *Etrema* sp. 1b, 11.5 mm. (72) *Etrema* sp. 1c, 6.5 mm. (73) *Etrema* cf. *polydesma* Hedley, 1923, 4.3 mm. (76) *Etrema* sp. 6, 6.7 mm. (75) *Etrema* aff. *crassilabrum* (Reeve, 1843), 8.5 mm. (76) *Etrema* cf. *crassilabrum* (Reeve, 1843), 11.6 mm. (77) *Etrema* cf. *glabriplicatum* (Sowerby III, 1913), 9.5 mm. (78) *Etrema* sp. 5, 4.0 mm.

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Plate 7

Figs 79-93: Raphitomidae. (79) *Hemilienardia homochroa* (Hedley, 1922), 3.8 mm. (80) *Hemilienardia malleti* (Récluz, 1852), 4.4 mm. (81) *Hemilienardia mikesevernsi* Wiedrick, 2017, 4.1 mm. (82) *Hemilienardia* cf. *gemmulata* Wiedrick, 2017, 6.9 mm. (83) *Hemilienardia calcicincta* (Melvill & Standen, 1895), 3.4 mm. (84) *Hemilienardia idiomorpha* (Hervier, 1897), 4.1 mm. (85) *Hemilienardia acinonyx* Fedosov *et al.,* 2017, 7.5 mm. (86) *Hemilienardia* sp., 4.0 mm. (87) *Hemilienardia shawnmilleri* Wiedrick, 2017, 5.0 mm. (88) *Pseudodaphnella* sp.10, 4.5 mm. (89) *Pseudodaphnella thereganum* (Melvill & Standen, 1896), 6.9 mm. (90) *Pseudodaphnella* sp. 12, 6.4 mm. (91) *Pseudodaphnella* sp.15, 5.9 mm. (92) *Pseudodaphnella* sp. 8, 6.5 mm. (93) *Pseudodaphnella tigroidella* (Hervier, 1896), 7.2 mm.

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Plate 8

Figs 94-108: Raphitomidae. (94) *Pseudodaphnella caletria* (Melvill & Standen, 1896), 6.0 mm. (95) *Pseudodaphnella* sp. 11, 4.3 mm. (96) *Pseudodaphnella* sp. 9, 7.3 mm. (97) *Pseudodaphnella* sp.14, 3.0 mm. (98) *Pseudodaphnella infrasulcata* (Garrett, 1873), 6.9 mm. (99) *Exomilus compressus* Fedosov & Puillandre, 2012, 3.6 mm. (100) *Pseudodaphnella spyridula* (Melvill & Standen, 1896), 2.9 mm. (101) *Exomilus edychrous* (Hervier, 1897), 3.2 mm. (102) *Kermia benhami* Oliver, 1915, 3.1 mm. (103) *Kermia* cf. *benhami* Oliver, 1915, 3.1 mm. (104-106) *Kermia* sp. 20., 3.3 mm, 2.9 mm, 3.3 mm. (107) *Pseudodaphnella granosa* (Dunker, 1871), 5.5 mm. (108) *Pseudodaphnella* aff. *drupelloides* (Kilburn, 2009), 3.5 mm.

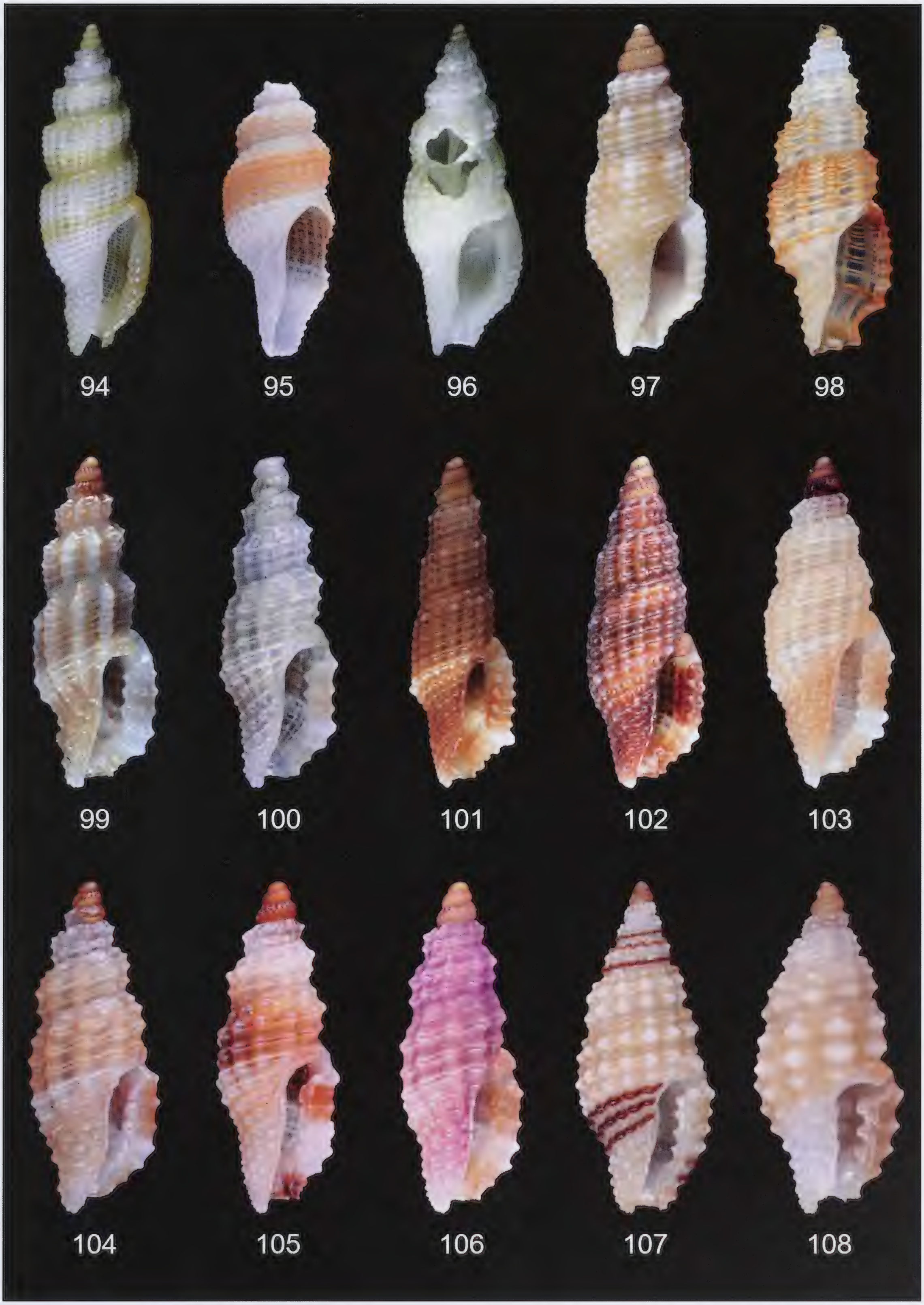
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Plate 9

Figs 109-123: Raphitomidae. (109) *Pseudodaphnella* sp. 21, 5.2 mm. (110) *Pseudodaphnella* cf. *barnardi* (Brazier,1876), 4.1 mm. (111 *Pseudodaphnella* cf. *tincta* (Reeve, 1846), 4.9 mm. (112) *Pseudodaphnella aureotincta* (Hervier, 1897), 7.0 mm. (113) *Pseudodaphnella fallax* Fedosov & Puillandre, 2012, 5.0 mm. (114) *Pseudodaphnella* aff. *lineata* Fedosov & Puillandre, 2012, 4.5 mm. (115) *Pseudodaphnella martensi* (G. Nevill & H. Nevill, 1875), 4.4 mm. (116) *Pseudodaphnella santoa* Fedosov & Puillandre, 2012, 5.3 mm. (117) *Kermia episema* (Melvill & Standen, 1896), 3.1 mm. (118) *Pseudodaphnella rubroguttata* (Adams, 1872), 8.3 mm. (119) *Pseudodaphnella* cf. *rubroguttata* (Adams, 1872), 6.1 mm. (120) *Pseudodaphnella* aff. *punctifera* (Garrett, 1873), 4.4 mm. (121) *Pseudodaphnella punctifera* (Garrett, 1873), 4.5 mm. (122) *Kermia melanoxytum* (Hervier, 1896), 5.7 mm. (123) *Pseudodaphnella caelata* (Garrett, 1873), 4.6 mm.

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Plate 10

Figs 124-138: Raphitomidae. (124) *Pseudodaphnella hadfieldi* (Melvill & Standen, 1895), 7.9 mm. (125) *Pseudodaphnella producta* (Pease, 1860), 4.9 mm. (126 *Pseudodaphnella daedalea* (Garrett, 1873), 6.8 mm. (127) *Pseudodaphnella* cf. *apicalis* (Montrouzier in Souverbie, 1861), 4.8 mm. (128) *Pseudodaphnella thespesia* (Melvill & Standen, 1896), 5.5 mm. (129) *Pseudodaphnella philippinensis* (Reeve, 1843), 16.9 mm. (130) *Tritonoturris cumingii* (Powys, 1835), 5.2 mm. (131) *Tritonoturris* sp. 1, 6.6 mm. (132) *Tritonoturris* cf. *subrissoides* (Hervier, 1897), 4.8 mm. (133) *Tritonoturris subrissoides* (Hervier, 1897), 8.1 mm. (134) *Tritonoturris lifouana* (Hervier, 1897), 7.2 mm. (135) *Daphnella* sp. 3, 5.0 mm. (136) *Daphnella vitrea* Garrett, 1873, 4.3 mm. (137) *Eucyclotoma* cf. *tricarinata* (Kiener, 1839), 4.7 mm. (138) *Eucyclotoma bicarinata* (Pease, 1863), 4.7 mm.

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Plate 11

Figs 139-153: Raphitomidae. (139) *Eucyclotoma carinulata* (Souverbie, 1875), 4.7 mm. (140) *Austrodaphnella torresensis* Shuto, 1983, 3.9 mm. (141) *Daphnella pluricarinata* (Reeve, 1845), 5.2 mm. (142) *Kuroshiodaphne* aff. *supracancellata* (Schepman, 1913), 15.2 mm. (143) *Daphnella ornata* Hinds, 1844, 11.7 mm. (144) *Diaugasma olyra* (Reeve, 1845), 8.0 mm. (145) *Daphnella canaliculata* Ardovini, 2009, 7.6 mm. (146) *Daphnella* sp. 2, 4.1 mm. (147) *Tritonoturris menecharmes* (Melvill, 1923), 11.7 mm. (148) *Veprecula* aff. *spanionema* (Melvill, 1917). (149) *Veprecula vacillata* Hedley, 1922, 4.9 mm. (150) *Veprecula* sp. 2, 4.9 mm. (151) *Veprecula* aff. *vepratica* (Hedley, 1903), 4.4 mm. (152) *Veprecula* sp.1, 5.8 mm. (153) *Microdaphne morrisoni* Rehder, 1980, 3.2 mm.

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Plate 12

Figs 154-166: Raphitomidae; Mangeliidae. (154) *Thetidos* cf. *morsura* (Hedley, 1899), 4.5 mm. (155) Raphitomid sp., 3.1 mm. (156) *Pleurotomella* cf. *itama* (Melvill, 1906), 4.9 mm. (157) *Eucithara* cf. *harpellina* (Hervier, 1897), 4.9 mm. (158) *Eucithara* cf. *lepidella* (Hervier, 1897), 6.8 mm. (159) *Eucithara cf. isseli* (G. Nevill & H. Nevill, 1875), 8.2 mm. (160) *Eucithara celebensis* (Hinds, 1843), 7.1 mm. (161-162) *Eucithara crystallina* (Hervier, 1897), 5.0 mm, 4.4 mm. (163) *Eucithara souverbiei* (Tryon, G.W. 1884), 5.2 mm. (164-165) *Gingicithara notabilis* (E. A. Smith, 1888), 3.9 mm, 3.4 mm. (166) *Heterocithara* sp. 13, 6.4 mm.

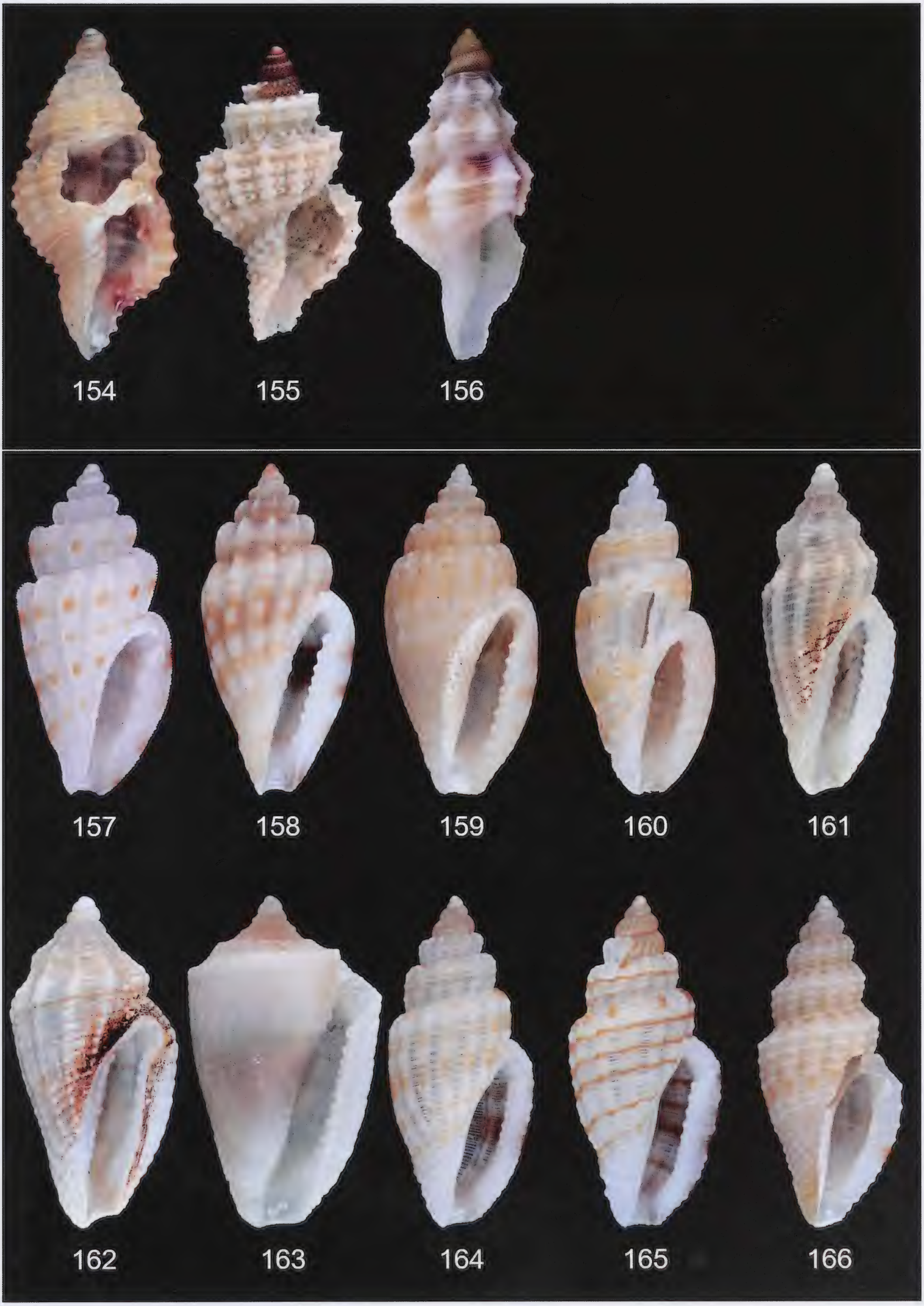
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Plate 13

Figs 167-181: Mangeliidae. (167) *Heterocithara strombillum* (Hervier, 1896), 3.5 mm. (168) *Heterocithara himerta* (Melvill & Standen, 1896), 5.3 mm. (169) *Heterocithara* sp. 14, 4.3 mm. (170) *Heterocithara* sp. 16, 3.6 mm. (171) *Heterocithara* sp. 17, 4.0 mm. (172-173) *Heterocithara isophanes* (Hervier, 1897), 4.2 mm, 3.8 mm. (174) *Heterocithara* sp. 18, 6.8 mm. (175) *Heterocithara diatula* Hervier, 1897, 3.3 mm. (176) *Heterocithara* sp. 19, 3.3 mm. (177) *Pseudorhaphitoma transitans* Hedley, 1922, 3.3 mm. (178) *Pseudorhaphitoma hervieri* Hedley, 1922, 5.0 mm. (179) *Macteola thalycra* (Melvill & Standen, 1896), 6.0 mm. (180) *Macteola* cf. *interrupta* (Reeve, 1846), 5.4 mm. (181) *Macteola* cf. *interrupta* (Reeve, 1846), juvenile 3.3 mm.

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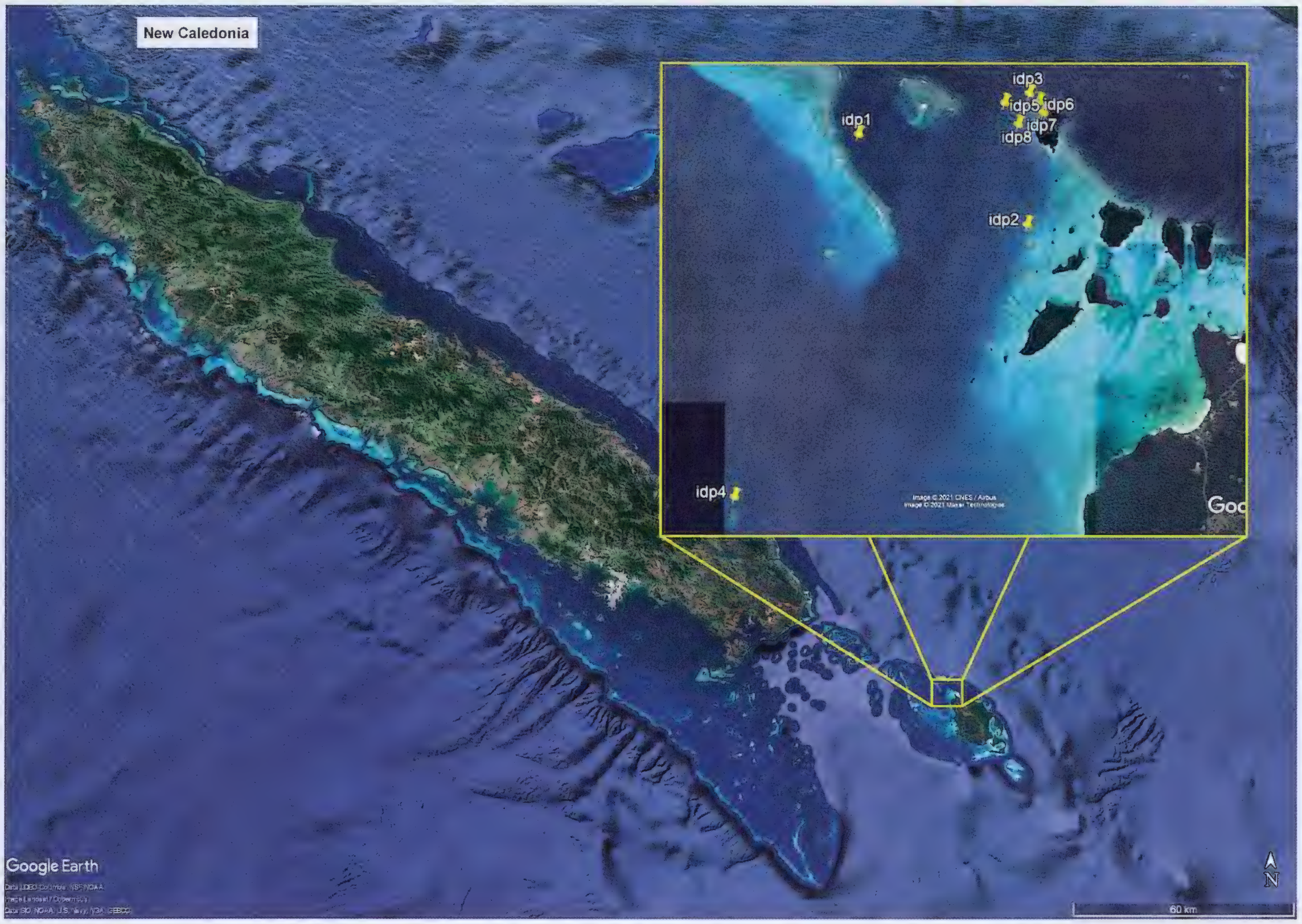
Annex 1: Overview of the sampling sites



Annex 2: Dive stations

Station	Latitude	Longitude	Depth min. [m]	Depth max. [m]	Date
idp1	22°31.054' S	167°23.383' E	8	20	03/02/2019
idp2	22°31.641' S	167°24.571' E	6	15	03/02/2019
idp3	22°30.787' S	167°24.586' E	16	27	04/02/2019
idp4	22°33.414' S	167°22.515' E	8	17	04/02/2019
idp5	22°30.848' S	167°24.412' E	16	27	05/02/2019
idp6	22°30.839' S	167°24.653' E	9	22	05/02/2019
idp3.2	22°30.787' S	167°24.586' E	24	25	07/02/2019
idp5.2	22°30.848' S	167°24.412' E	22	24	07/02/2019
idp7	22°30.912' S	167°24.684' E	13	23	08/02/2019
idp8	22°30.989' S	167°24.508' E	6	21	08/02/2019
idp piscine	22°35'2.22»S	167°31'40.72»E	0.5	2	06/02/2019

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The description of a new species of *Anarthrotarsus* Šilhavý from Greece and a discussion about the genus (Arachnida: Opiliones: Trogulidae)

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Abstract: *Anarthrotarsus trichasi* sp. nov., a second species of the genus *Anarthrotarsus* Šilhavý, 1967 is described based on fresh material from the northeastern part of the island of Crete, Greece. The male holotype of the type species of the genus *Anarthrotarsus* was discovered on the island of Corfu, Ionian Islands, Greece, but no other conspecific specimens were found there ever since. This also holds true for the population from Crete, from where a female paratype was collected. Genital morphology of male specimens from both populations markedly differs, and that of the holotype from Corfu is even unique among Trogulidae. Though the tarsal formula (1-1-1-1 in the four walking legs) is identical in both populations, penis morphology, the main generic character of *Anarthrotarsus*, clearly separates them. A close relationship of *A. trichasi* sp. nov. with species of the genus *Calathocratus* Simon, 1879 is supposed but awaits molecular genetic affirmation.

Keywords: Generic systematics - genital morphology - relationships - cryptic species - Crete - Corfu.

INTRODUCTION

The family Trogulidae has a paleo-Mediterranean distribution and occurs all over this region from northern Africa and the Iberian Peninsula eastwards to the Near East, i.e. to the Caucasus countries (Šilhavý, 1966; Staręga, 1966) and Turkey (Gruber, 1968; Schönhofer *et al*., 2013), and northwards to the Alps and central Europe (Martens, 1978). Eastwards the species' diversity fades out in the Iranian Alborz Mts (Snegovaya *et al*., 2021), Kyrgystan (Tchemeris, 2013) and Tajikistan (specimens in CJM) where only isolated species from widely separated localities are present. To date the family comprises five genera and 56 species (Schönhofer, 2013). Three genera include the majority of species, especially *Trogulus* Latreille, 1802 (32 species), *Anelasmocephalus* Simon, 1879 (13 spp.) and *Calathocratus* Simon, 1879 (9 spp.). For Greece ten trogulid species (Chatzaki, 2020) have been determined, but due to the puzzling homogeneity of external and partly genitalic characters, species delimitation is often difficult to establish, sometimes it is simply impossible. Modern molecular genetic analyses proved the diversity of species to be much larger than formerly believed. In recent years, ten species of *Trogulus* new to science were identified in various Mediterranean countries and were described; several more await disentanglement and formal description (Schönhofer & Martens, 2008, 2009; Schönhofer *et al*., 2013). On the other hand, the genera *Platybessobius* Roewer, 1940 and *Trogulocratus* Roewer, 1940 were synonymized with genus *Calathocratus*, again on the basis of a genetic analysis (Schönhofer & Martens, 2010). This taxonomic act was particularly striking as these three nominal genera were clearly separated by distinct tarsal formulas, i.e. the number of tarsal articles on the walking legs I-IV. Tarsal formulas are believed to clearly characterize and define the genus *Trogulus* and the closely related (and allopatric) species within various species groups in *Anelasmocephalus*. The newly circumscribed genus *Calathocratus* now comprises species with different tarsal formulas, and a close relationship among them is clearly shown by molecular data (Schönhofer & Martens, 2010). Also, in *Calathocratus,* the hidden diversity is enormous. Schönhofer & Martens (2010) identified nine more or less widely separated *Calathocratus* clades from Italy to Turkey and the Caucasus, of which

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at least the majority merits species rank. Most of them are still undescribed due to the difficulty to elucidate morphological distinctions, which are important for species identification beyond genetics.

Anarthrotarsus is an enigmatic trogulid genus from Greece. It was erected by Šilhavý (1967) based on a male specimen from Corfu, the holotype, and a female from eastern Crete. No further specimens were collected ever since, therefore a genital morphological comparison of specimens from these widely separated populations was not possible. The drawings of Šilhavý (1967) already indicated that the penis morphology of the type species, *A. martensi* Šilhavý, 1967, is quite peculiar and very distinct from any other trogulid species. Schönhofer & Martens (2010) were unable to incorporate *Anarthrotarsus* in an extensive phylogenetic study about trogulids based on molecular genetics due to the lack of fresh material. Recently, new material of both sexes of the Cretan population became available to us, and it is now evident that the holotype and paratype of *A. martensi* do not belong to the same species. Therefore, the population from Crete deserves a new status and name, which we give here.

MATERIAL AND METHODS

The examined material originated from the Opiliones collection of the Natural History Museum of Crete and was obtained during NHMC expeditions in eastern Crete in October to December of 1997 and January to March of 2008. The sampling method was pitfall trapping, as described in Salata *et al*. (2020).

Original line drawings were produced using a camera lucida attached to a Carl Zeiss research microscope. The photographs (Figs 1-2) were taken with a Canon 5D with a MP-E 65 mm f/2.8 1-5x Macrolens. Measurements were taken by means of a micrometer disc attached to a Leica M165C stereomicroscope. All measurements are given in mm.

The distribution map was created with the software QGIS 3.16.

Abbreviations of morphological terms

Cl	claw
Cx	coxa
FC	field code (sample number)
Fe	femur
L	leg
Mt	metatarsus
Pt	patella
Ta	tarsus
Ti	tibia
Tu oc	tuber oculorum, ocularium
Tr	trochanter

Museum acronyms

CJM	Private collection of J. Martens, Mainz, Germany, to be transferred to the SMF
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
NHMC	Natural History Museum of Crete, University of Crete, Heraklion, Greece
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

TAXONOMIC PART

Suborder Dyspnoi Hansen & Sørensen, 1904
Family Trogulidae Sundevall, 1833
Genus *Anarthrotarsus* Šilhavý, 1967

Type species: *Anarthrotarsus martensi* Šilhavý, 1967 by monotypy and original designation.

Species included: *Anarthrotarsus martensi* and *A. trichasi* sp. nov.

Anarthrotarsus trichasi sp. nov.

Figs 1-15

Anarthrotarsus martensi Šilhavý, 1967: 176 (in part, only female paratype).

Holotype: NHMC 81.5.619.1; male; GREECE, Crete, Lasithi, 2 km behind Moni Toplou, on the way to Vai, 35.2365°N 26.2273°E, 170 m alt.; 11.8.-14.12.1997; leg., I. Stathi (sample FC 619).

Paratypes: CJM 8994; 4 males, 1 female; collected together with the holotype. – CJM 8995; 2 males, 2 females; GREECE, Crete, Lasithi, Pacheia Ammos, 500 m east of village, 35.1094°N 25.8183°E, 20 m alt; 20.1.-16.3.2008; leg. D. Kaltsas (sample FC 9257). – NHMC 81.5.619.2; 1 male; same data as for the holotype. – MHNG; 1 male; same data as for the holotype. – SMF 19699; 1 female (paratype of *Anarthrotarsus martensi*); Siteia Bay [= Bucht von Sitia]; 11.3.1966; leg. H. Pieper.

Comparative material: SMF RII/7450; male holotype of *Anarthrotarsus martensi.* – CJM 5730; 1 specimen of *Calathocratus beieri* Gruber, 1968; TURKEY, Adana, Kozan-Feke; 25.4.2007; leg. Brachat & H. Meybohm. – CJM 7134; 1 specimen of *Calathocratus rhodiensis* (Gruber, 1963); GREECE, Rhodos, Profitis Ilias; 3.4.2012; leg. H. Meybohm. – CJM 1719; 3 specimens of *Calathocratus* sp.; MOROCCO, Tafoughalt; 30.9.2010; H. Wijnhoven. – CJM 5665; 1 specimen of *Calathocratus africanus* (Lucas, 1849); ITALY, Sicily, Piazza Armerina; 1.5.2009; H. Wijnhoven. – CJM 3039; 19 specimens of *Calathocratus kyrghyzicus* (Tchemeris, 2013); KYRGYSTAN, Sary-Celek Nature Reserve; 29./30.5.1993; leg. J. Martens. – CJM 3453;

Figs 1-2. *Anarthrotarsus trichasi* sp. nov. (1) Body in dorsal view. (2) Legs III and IV in prolateral view. Scales: 1.0 mm. Photographs by A. Trichas.

1 specimen of *Calathocratus* sp.; IRAN, Masanderan; 31.5.1978; leg. J. Martens. – CJM 2464; 1 specimen of *Calathocratus* sp.; ISRAEL, Hazafon, Lower Galilee; 9.2.1987; leg. W. Schawaller & H. Schmalfuß. – CJM 6586; 3 specimens of *Calathocratus* sp.; TAJIKISTAN, Sary-Khosor State Reserve; 28.4.1990; leg. S. Dashdamirov.

Diagnosis: A small (4.1-4.4 body length) and slender (1.3-1.5 body width) species with thin and delicate legs (more so than in *A. martensi*); short and stout pedipalps; penis parallel-sided (ventral/dorsal views), with elongate glans sparsely covered with bifid setae.

Name: The species epithet is a name (in the genitive case) in honour of Dr Apostolos Trichas, coleopterologist and curator of Arthropoda at the Natural History Museum of Crete, Greece.

Description: MALE (paratype CJM 8995). *Body, dorsal side* (Fig. 1): Colour varying from yellowish brown to hazel-brown partly due to slight incrustations from the ochre-coloured soil at the collecting localities; body small and slender; increased density of circular, hemispherical papillae extending from eye mound to remainder of body; small and narrow head cup (approximately 0.5 in diameter) in comparison with total body length, with a downward slope and with poorly developed Tu oc (approximately 0.8 in diameter); eye interdistance short (0.29).
Body, ventral side: Increased papillation and the same proportion as on the dorsal side.

Fig. 3. *Anarthrotarsus trichasi* sp. nov.; localities on the island of Crete: 1 - Pacheia Ammos; 2 - Siteia Bay; 3 - Moni Toplou. White line indicates eastern border of the Dikti Mountain Range.

Figs 4-15. *Anarthrotarsus trichasi* sp. nov., male paratype CJM 8995. (4-6) Penis in ventral, dorsal and lateral view, respectively. (7-9) Glans penis in ventral (7), lateral (8) and dorsal view (9; arrow pointing to enlarged illustration of bifid seta). (10) Right pedipalp in pro-lateral view. (11) Right chelicera in retro-lateral view. (12-15) Tarsi with claw in pro-lateral view: leg I (12), leg II (13), leg III (14), leg IV (15). Scales: 0.3 mm (4-6), 0.05 mm (7-9), 0.1 mm (10), 0.2 mm (11-15).

Chelicera (Fig. 11): First article small (0.68 long) and slender, tapering from base to distal end, with a slight enlargement on ventral side; 2nd and 3rd article slender (0.25 and 0.31 long, respectively) as well, their setation sparse, longest setae on 2nd article on frontal side; size and proportion of chelicerae typical for small species of trogulids.
Pedipalp (Fig. 10): Short (0.88) and stout; Pt slightly enlarged in distal part; less obviously so in Ti; Ta cone-shaped, its distal part with a slight pseudo-articulation. Elongated setae more dense on Ti and Ta than on other articles.
Legs (Figs 2, 12-15): With increasing papillation and setation, especially on metatarsi and tarsi; apophyses on disto-dorsal surface of metatarsi most elongated in legs III and IV; tarsal articles of various sizes, longest in leg II; claws more or less distinctly hook-shaped, claw on leg I very robust and almost as large as tarsal article; smooth setae on all tarsi, including single long setae dorsally and distally. Several fine setae beneath the claw on tarsi I-III inflected upward in their distal part.
Genital morphology (Figs 4-9): Penis relatively short and slender; truncus nearly parallel-sided (in dorsal and ventral views), slightly tapering towards distal end in lateral view; glans slender, tapering towards stylus, sparsely covered with relatively short and stout setae, slightly forked at tip (see detail in Fig. 9); stylus slightly bent sidewards (in dorsal and ventral views).
FEMALE. General somatic morphology as in males, body dimensions slightly larger.

Measurements: Body length of males 4.1-4.4 (n=7) (average length 4.2), of female 4.68 (n=1). Penis length 0.98-1.11 (n=7) (average length 1.1). Measurements of legs and pedipalps see Table 1.

Variation: The specimens of *A. trichasi* sp. nov. examined do not appear to vary markedly in their somatic features. The male genitalia show very little variability in glans proportions as well as in the density of the setae cover.

Relationships: See Discussion.

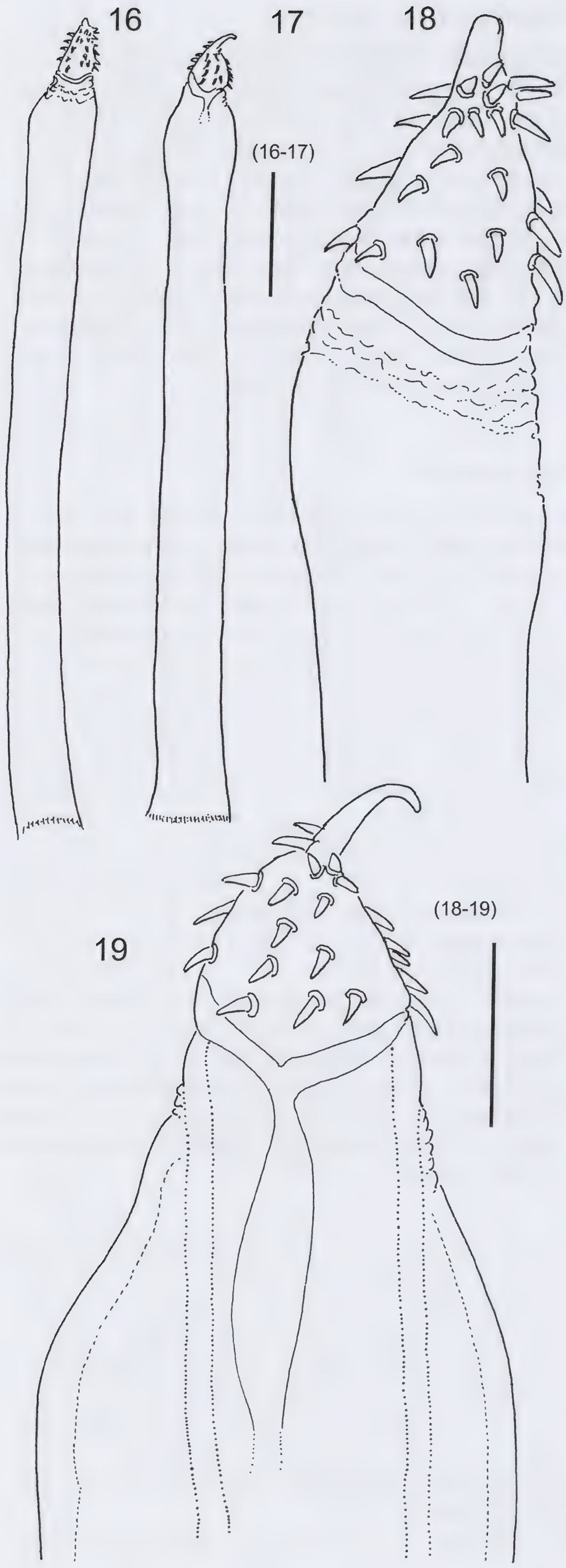
Distribution and habitat preferences: The species is only known from three localities in the eastern part of the island of Crete (Lasithi Province), from near the coast to about 170 m altitude (Fig. 3). The female paratype of *A. martensi* from the Bay of Siteia, which we attribute to *A. trichasi* sp. nov. and designate it as a paratype of the latter, is within this altitudinal and geographic range. These three sites are characterized by dry vegetation such as groves of juniper (*Juniperus phoenicea* L.) and phrygana with hard-leaved and cushion plants like, e.g., the prickly burnet *Sarcopoterium spinosum* (L.) Spach.

DISCUSSION

Single references to trogulids in Greece date back to Roewer (1940, 1950) but the species there have never been studied in any detail. Schönhofer (2013) mentions seven species, a relatively small number for a Mediterranean country, Chatzaki (2020) ten species. Species of *Trogulus* occur over large parts of the country including the Aegean Islands, all are presently attributed to one or two species names. A large amount of cryptic species is assumed to be present, but details are unavailable at present. The situation of the Cretan trogulid fauna is somewhat complicated though only few species are concerned. Roewer (1940) described *Calathocratus intermedius* (Roewer, 1940) and *C. singularis* (Roewer, 1940), all from the western part of the island. The collecting circumstances of these records are somewhat doubtful (see Helversen & Martens, 1972) and have never been clarified. A molecular genetic study identified two closely related but clearly separated populations of *C. singularis* within Crete and another one from the Peloponnese (Schönhofer & Martens, 2010); their taxonomic status is unclear. The latter authors also mention a *Trogulus* locality on Crete, Deliana, of unclear species affiliation ("*T.* aff. *gypseus*").

Table 1. Measurements of pedipalp and legs of male (paratype CJM 8995) and female (in parentheses, paratype CJM 8994) of *A. trichasi* sp. nov.

	Tr	Fe	Pt	Ti	Mt	Ta	Cl	Total
Pedipalp	0.11 (0.10)	0.28 (0.25)	0.12 (0.10)	0.21 (0.20)	-	0.16 (0.15)	-	0.88 (0.80)
L I	0.35 (0.32)	0.75 (0.71)	0.41 (0.40)	0.50 (0.46)	0.49 (0.50)	0.13 (0.10)	0.11 (0.11)	2.74 (2.60)
L II	0.41 (0.44)	1.40 (1.40)	0.55 (0.54)	0.96 (0.95)	1.10 (1.08)	0.43 (0.40)	0.06 (0.07)	4.91 (4.88)
L III	0.34 (0.33)	0.84 (0.85)	0.42 (0.44)	0.78 (0.70)	0.74 (0.70)	0.19 (0.15)	0.10 (0.10)	3.41 (3.37)
L IV	0.54 (0.52)	1.30 (1.25)	0.58 (0.55)	0.97 (0.92)	0.99 (0.95)	0.21 (0.20)	0.13 (0.14)	4.72 (4.43)



Figs 16-19. *Anarthrotarsus martensi,* male holotype. (16-17) Penis in dorsal (16) and ventral view (17). (18-19) Glans in dorsal (18) and ventral view (19). Scales: 0.3 mm (16-17), 0.05 mm (18-19).

Among all these uncertainties, there is the single female specimen of *Anarthrotarsus martensi*, published already in 1967 (Šilhavý, 1967), the only record for this species until recently. Now males are available for study, and male genital morphology of specimens from both populations turn out to be remarkably different, and their status as separate species is evident. The male type specimen (allegedly) of *A. martensi* from Corfu is considerably smaller (3.95 body length) than males of *A. trichasi* (4.1-4.4 body length) and has a subdistally notably enlarged truncus (Figs 16-19), as well as a short glans covered by a loose array of short and stout setae. In contrast, the also distally parallel-sided penis of *A. trichasi* sp. nov. and its longish glans with only scattered bifid setae differ markedly. The distinct differences between the Corfu and Crete population raise the question whether both populations can at all be associated to the same genus. This is at least doubtful. The molecular genetic analysis of Schönhofer & Martens (2010) did not include either population, and the question remains open. A close relationship of *A. trichasi* sp. nov. with populations of *Calathocratus* is possible because of a strong similarity in their genital morphology. But the latter genus, with a distribution from northern Africa to Italy, the Balkans and Turkey and further east, is heterogeneous in itself and requires a detailed molecular and morphological study. For the time being we associate both species in question to *Anarthrotarsus* and expect clarification of the situation from a comprehensive molecular genetic study. As for the zoogeographical point of view, *A. trichasi* is recorded from three distant localities in Lasithi Province. All of these records are from the easternmost part of the island, without the Dikti Mts intervening and all east of this mountain range, which indicates an important role of these mountains as a biogeographical barrier between the east and the west of the island. Moreover, since the areas surrounding the *A. trichasi* localities are also covered with dry open shrublands, the distribution of this species may be more extensive than it is reported here. However, although information is still limited, we consider *A. trichasi* sp. nov. to be a small-scale endemic species of the eastern-most part of Crete.

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Revision of the genus *Parasyleter* Balkenohl, 2021 with the descriptions of four new species (Coleoptera: Carabidae: Clivinini)

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Abstract: The genus *Parasyleter* Balkenohl, 2021 is revised. For the type species *P. doriae* (Putzeys, 1873) a lectotype is designated in order to maintain stability of the nomenclature. The following new species are described: *P. perak* sp. nov., *P. kerdil* sp. nov., *P. rastellus* sp. nov., and *P. livaguensis* sp. nov. An identification key to the species is provided. The distribution records of the species are displayed on a map.

Keywords: Oriental region - taxonomy - lectotype designation - key to species.

INTRODUCTION

Recently, a complex Oriental species group formerly summarized in the genus *Syleter* Andrewes, 1941 was redefined with a split up into the three genera *Syleter* Andrewes, 1941, *Parasyleter* Balkenohl, 2021, and *Clypeuspinus* Balkenohl, 2021. In the same contribution the genera *Syleter* and *Clypeuspinus* were revised, and keys to the three genera and to the species of *Syleter* were provided (Balkenohl 2021). *Syleter* comprises six species and one subspecies whereas *Clypeuspinus* is a monotypic genus.

The genus *Parasyleter* consists of small sized species (1.8 to 2.4 mm) and some species show a significant reduction of the eyes and hind wings. Specimens are rarely represented in Museums and other collections, and if so there are often only one or few specimens available. Over ninety years ago, three species were described, *P. doriae* (Putzeys, 1873), *P. porphyreus* (Andrewes, 1923), and *P. malayicus* (Andrewes, 1927).

This contribution has the goal to revise the genus *Parasyleter,* to provide a key to the species, and to summarize the distribution.

MATERIAL AND METHODS

Terms, descriptions of characters, methods, microscopy and photographs are described in Balkenohl (2021).

For the revision 59 specimens including types and other material were investigated. In general, all additional informative material like original paper cards and pins have been kept at the specimens. The collecting information of the examined specimens like date, locality and collector is cited as given on the original labels. For the descriptions, the length was measured from the most anteriorly projecting part of the head (clypeus at middle or clypeal wings) and does not include the elongated mandibles. The length of the pronotum was measured along the median line and includes the posteriorly elongated flange. The width of the pronotum and elytra was measured at the maximum width. The description of the genitalia refers to the natural position the genitalia exhibit in soaked specimens before they are extracted, cleaned, and mounted.

For the species described already, an extended diagnosis is provided to include additional data and to clearly discriminate the species.

Abbreviations used:

ADCW	Alexander Dostal collection (including Coll. Karel Kult), Vienna, Austria
BMNH	Natural History Museum, London, United Kingdom
MBCB	Michael Balkenohl working collection, Bonstetten, Switzerland
MFNB	Museum für Naturkunde Berlin, Germany
NHMW	Naturhistorisches Museum, Wien, Austria
MHNG	Muséum d'histoire naturelle, Genève, Switzerland
MNHN	Muséum national d'Histoire naturelle, Paris, France
PBCP	Petr Bulirsch Collection, Prague, Czech Republic

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RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
[…]	in brackets: additional information by the author
/	slash: separates different labels or values under measurements
$\bar{x}$	arithmetic mean (used in the measurements for the descriptive statistics)

TAXONOMY

Order Coleoptera
Family Carabidae Latreille, 1802
Subfamily Scaritinae Bonelli, 1810
Tribe Clivinini Rafinesque, 1815
Genus *Parasyleter* Balkenohl, 2021

Parasyleter Balkenohl, 2021: 358.

Type species: *Dyschirius doriae* Putzeys, 1873: 14.

Genus diagnosis: *Size* 1.8 to 2.3 mm. *Head* with clypeus and frons distinctly elongated and flattened anteriorly; clypeus and clypeal wing fused, delimitation between clypeal wing and supraantennal plate observable as indistinct obtuse notch in two of the species; clypeus straight or slightly convex anteriorly, as far as or slightly more projecting than clypeal wing; mandible elongate, narrow in apical third, laterally nearly straight or convex, hooked at apical tip; labrum five- or seven-setose; maxillary palpomere distinctly narrowed and slender towards apex, nearly straight, two apical segments securiform; antenna with scapus and pedicellus eccentrically attached; eye without or with distinct reduction, gena small or extended posteriorly. Mentum not elongated, with lateral lobe convex, median tooth as wide as lateral lobe, acute, distinctly more projecting than lateral lobe, surface with slight transverse rugae. *Pronotum* square or indistinctly trapezoid, with reflexed lateral margin incomplete, running from anterior angle up to posterior setigerous puncture, posterior angle rounded off without tooth, lateral channel of equal width, median line narrow, finely or just not joining basal constriction; proepisternum visible basally in dorsal view; flange at base convex, as narrow as or up to two times as wide as basal constriction. *Elytron* with interval eight convex, lateral channel distinctly flared apically, with interval eight distinctly emarginated apically and row of umbilical setigerous punctures distinctly following the emargination, interval eight with distinct emarginated carina at apex; third interval without setigerous punctures. *Hind wings* fully developed or reduced. *Legs* with front and intermediate tarsomeres slightly widened, more distinct in males; mesotibia with four setae laterally, preapical seta either without any protuberance or arising from minute tubercle. *Male genitalia* with aedeagus distinctly curved, apical part elongated, apex more or less spatulate or securiform. *Female genitalia* with gonocoxite one and two completely fused, with evident cone-like seta in apical third; laterotergite with isolated setae.

Differential diagnosis: See key to the genera in Balkenohl (2021).

Parasyleter doriae (Putzeys, 1873)
Figs 1, 2, 9, 10, 16, 20

Dyschirius doriae Putzeys, 1873: 14.
Dyschirius doriae. – Csiki, 1927: 525. – Csiki, 1933: 639.
Psilus doriae. – Andrewes, 1927: 267. – Andrewes, 1930: 287.
Syleter doriai. – Jeannel, 1957: 138.
Syleter doriai. – Lorenz, 1998: 138. – Lorenz, 2005: 148.
Syleter doriae. – Balkenohl, 2001: 30, fig. 40. – Balkenohl, 2021: 369, with 5 figs.

Type material examined: *Lectotype* by present designation: RBINS; ♂, with labels and data: grey, black framed, handwritten in black ink "Borneo Sarawak 1865-66. Coll. G. Doria", and backside "Kantu" / grey, handwritten in black ink and printed "Dyschirius doriae PUTZ. dét. J. Putzeys" / grey, black framed and black printed "Soc.Ent.Belg. Coll. Putzeys" / white, black framed, red printed "Syntype".
Paralectotypes by present designation: RBINS; 1 ♂, 2 specs., same data as lectotype, one with additional white label and handwritten in black ink and printed "Psilus doriae Putz. Cotype H.E.Andrewes det. 1928". – MFNB; 1 ♂, with labels and data: grey, black framed, handwritten in black ink "Borneo Sarawak 1865-66. Coll. G. Doria", and backside "Kantu" [same as lectotype] / grey, printed "160" / white, printed "61302" / white, printed "Zool. Mus. Berlin" / yellow, handwritten in black ink "Doriae Putz.". – BMNH; 1 ♂, with labels and data: grey, black framed, handwritten in black ink "Borneo Sarawak 1865-66. Coll. G. Doria", and backside "Kantu" [same as lectotype] / white, handwritten in black ink "Ex Mus. Civ. Genova" / handwritten in black ink and printed "Psilus doriae Putz. Compared with Cotype H.E.A." [H.E.Andrewes]. – MNHN; 1 ♂, same data as the last one.

Additional material: MFNB; 1 ♀, Sarawak / Dyschirius Doriae / Coll. L.W. Schaufuss / Zool. Mus. Berlin. – MFNB; 1 ♀, S.O. Borneo Grabowsky. / Zool. Mus. Berlin. – ADCW; 1 ♀, INDONESIEN: Kalimantan Timur, Tanjung Isuy 20.1.1995 leg. Seyfert & Greindl (33) / Coll. Zettel Wien. – BMNH; 1 ♀, Borneo Ban…. [not readable] / 56237 / Fry Coll. 1905.100. / Psilus doriae Putz. Compared with type H.E.A. [found glued]. – ADCW; 2 ♂, 8 ♀, S Thailand, Betong Gunung Cang dun vill. Yala dist., 25.3.-22.4.1993 J. Horák leg.". – NHMW; 2 ♀, same data as

Identification key to the species of the genus *Parasyleter*

1A Eye conspicuously reduced, consisting of few ommatidida, surrounded by a distinct ring of dark pigment; gena large, projecting laterally as high as eye; species without hind wings 2
1B Eye convex, consisting of numerous ommatidida; gena small; species with or with conspicuously reduced hind wings 4
2A Outline of elytron regularly ovate; eye projecting anteriorly; gena 2.5-3 three times as long as eye; elytron with intervals flattened, punctures of striae slightly deepened, distinctly shortened apically, striae one and two free at base; colour testaceous to rufous; body length 1.8 mm. West Malaysia: Lake Kenyir ..... ***kerdil*** sp. nov.
2B Outline of elytron oval but wider at humeri and apically; eye directed anterio-laterally; gena 1.5 or 2 three times as long as eye; elytron with intervals slightly convex, punctures of striae deepened, reaching the apical fifth, striae one to three free at base; colour fulvous or piceous; body length more than 1.9 mm 3
3A Pronotum conspicuously square, median line shallow; colour piceous; elytron with punctures of striae moderately deep; interval eight of elytron wider as seven; body length 2.1-2.2 mm. West Malaysia: Perak ..... ***perak*** sp. nov.
3B Pronotum sub-trapezoid, median line distinct; colour fulvous; elytron with punctures of striae deepened; interval eight of elytron as wide as seven. Body length 1.9 mm. West Malaysia: Island of Penang ..... ***malayicus***
4A Labrum 7-setose; lateral margin of elytron smooth; outline of pronotum longitudinal sub-trapezoid; wings of clypeus slightly projecting anteriorly; male aedeagus slightly curved. Body length 2.4 mm. Sri Lanka, southwestern provinces..... ***porphyreus***
4B Labrum 5-setose; lateral margin of elytron serrulate; outline of pronotum globose to sub-trapezoid; wings of clypeus as projecting as clypeus 5
5A Serrulation at the lateral margin of the elytron in anterior half nearly invisible; lateral margin and channel of pronotum narrower at middle, disk laterally with longitudinal group of small punctures. Body length 2.3-2.6 mm. Malaysia, Sabah ..... ***livaguensis*** sp. nov.
5B Serrulation at the lateral margin of the elytron well visible in anterior half; lateral margin and channel of pronotum of same width from anterior to posterior setigerous puncture, disk smooth 6
6A Clypeal field U-shaped, covered with isodiametric reticulation, with transverse clypeal furrow in form of a flattened letter V; labrum concave; lateral margin of elytron indistinctly convex and diverging. Male aedeagus at apex with elongated spatula. Body length 2.1-2.5 mm. Borneo, Malay Peninsula, Sumatra ..... ***doriae***
6B Clypeal field square, smooth, with transverse clypeal furrow straight; labrum straight; lateral margin of elytron straight in anterior half but diverging. Male aedeagus at apex with short flattened hoe. Body length 2.2-2.4 mm. Laos, Cambodia, South of Vietnam ..... ***rastellus*** sp. nov.

the last one. – PBCP; 3 ♀, same data as the last one. – PBCP; 1 ♀, same data but 4-93 leg. Strnad. – PBCP; 1 ♀, MALAYSIA; JAHOR; 50-400m; Endau-Rompin; 19.iii.1998; Pulau Jasin; 2,31N 103,21 E / backside leg. Hauk. – NHMG; 2 ♂, 1 ♀, MALAYSIE Pahang Temerloh 9. III. 77 T. Jaccoud. – NHMG, MBCB; 1 ♂, 1 ♀, Malaisie Selangor Kuala Lumpur 25.8.69 R. Pilet Plantation d'Heveas. – MNHN; 1 spec., Sumatra Palembang / Dr. Forster / Syleter doriae Putz. [glued spec. in desolate condition with separately mounted but empty hind body].

Extended diagnosis: *Head* anterior eyes distinctly elongated, with impressed transverse clypeal furrow in form of a flattened letter V and with few rugae laterally; clypeal field U-shaped, covered with indistinct isodiametric reticulation, separated from anterior margin of clypeus by distinctly isodiametric reticulated flat area, fused with clypeal wings, straight anteriorly, with indistinct obtuse notch to supraantennal plates; supraantennal plates keeled; frontal furrows moderately deep; frons smooth, with small circular pore, laterally with tubercle-like longitudinal carinae; neck constriction developed laterally as row of few punctures, with wide gap at middle; labrum slightly concave, five-setose; mandible distinctly elongated; eye somewhat reduced but still of moderate size in lateral view, somewhat flattened in dorsal view, slightly surrounded by dark pigment; gena small. *Pronotum* sub-trapezoid to globose, slightly wider than long, slightly narrowed in anterior half, posterior angle completely rounded off; reflexed lateral margin ending at posterior setigerous puncture; flange convex, two times as wide as basal constriction; disk smooth, median line narrow, joining with anterior transverse line and finely with basal constriction as line of dark pigment. *Elytron* nearly 1.5 times longer than wide, with indistinctly convex but slightly diverging margin anterior middle, maximum width slightly posterior middle of elytron; humerus well visible; reflexed lateral margin serrulate from sharp humeral tooth nearly up to apex; interval eight slightly wider than seven; striae distinctly punctate, profound; lateral channel somewhat narrower at middle with umbilical setigerous punctures of equal distance, at apex conspicuously widened by

Figs 1-8. *Parasyleter* spp., habitus. (1) *P. doriae* (Putzeys, 1873), paralectotype, from Sarawak, male. (2) *P. doriae,* male specimen from Betong Gunung, South of Thailand. (3) *P. porphyreus* (Andrewes, 1923), holotype, female. (4) *P. malayicus* (Andrewes, 1927), holotype, male. (5) *P. perak* sp. nov., holotype, male. (6) *P. kerdil* sp. nov., holotype, female. (7) *P. rastellus* sp. nov., holotype, male. (8) *P. livaguensis* sp. nov., holotype, male.

emargination of interval eight which is costate apically. *Hind wings* see variability. *Legs* with protarsomeres slightly widened in both sexes. *Male genitalia* (Figs 9, 10) with aedeagus in ventral view slightly curved in basal half, distinctly curved and elongated apically, at apex with conspicuously elongated flattened spatula; in lateral view widened at middle, apical spatula distorted, turned ventrally, widened to tip, internal sac at middle with bunch of bristles, antero-laterally with eight large longitudinal spines; ventral paramere oval, wide, slightly acuminated at tip, both parameres asetose. *Female genitalia* (Fig. 6) with gonocoxites regularly curved to apex, robust in apical half, base stout; with moderately sized cone-like seta anterior middle, ventromedially with eight nematiform setae; laterotergite with three moderately long nematiform setae. *Measurements.* Body length 2.16-2.48 mm ($\bar{x}$: = 2.28 mm*), width 0.81-0.85 mm ($\bar{x}$: = 0.82 mm*), ratio length/width of pronotum 0.86-0.9 ($\bar{x}$: = 0.88*), ratio length/width of elytra 1.53-1.62 ($\bar{x}$: = 1.58*); (*n = 12).

Variability: The pore on the frons of head is more or less distinctly developed. The reticulation on the clypeal field is more or less distinct, the furrow separating the clypeus from frons is more or less impressed. Specimens from West Malaysia have the labrum more straight. Specimens from Borneo seem to have slightly less elongated elytra. Some specimens from Borneo show reduced hind wings. This character was not observed in specimens from West Malaysia. It is hypothesized that wing dimorphism is present in some populations.

Distribution: Known to be distributed on Borneo, the Malay Peninsula from the South of Thailand to the South of the Peninsula, and from Sumatra (Fig. 20).

Type locality: Borneo, Sarawak.

Remarks: In his half-page quite correct description, Putzeys (1873) did not mention on how many specimens he based the description on. It is also unclear to which collections specimens were distributed. However, the investigated seven specimens show identical labels with the same handwriting and kind of mounting. Therefore, these specimens are regarded to be part of the type series.

Andrewes reports the 'type' of *doriae* "should be" in the museum of Genova but is missing there, but a 'cotype' is at Brussels (Andrewes 1926, p. 378). Five of the seven 'syntypes' were located in RBINS, one in the BMNH and in the MNHN, each.

The species was described as *Dyschirius doriae* Putzeys (Putzeys 1873) and transferred into the genus *Psilus* Putzeys by Andrewes (1927). Later, Andrewes (1941) renamed *Psilus* into *Syleter* due to preoccupation. The species is listed as *doriae* in Csiki (1927: 525, 1933: 639), Andrewes (1930: 287), and Balkenohl, 2001: 31. However, in Jeannel (1957: 138), and Lorenz (1998: 138, 2005: 148) it is listed as 'doriai'.

Dyschirius, Psilus, and *Syleter* are masculine genus names. The description in Putzeys (1873) clearly indicates the species was delivered by M. le marquis Doria. In the same volume it is mentioned Marquis Doria was the director of the Museo civico di Storia naturali - Gènes (p. CLXXI). Therefore, the dedication to Marquis Giacomo Doria is verified and not to a woman with the name of 'Doria' is intended. This would lead to the assumption the name is not correctly formed according to the conditions of ICZN Article 31.1.2. (1999). However, the name is not an adjective but a substantive in the genitive case and remain therefore independent from the grammar form of the genus. According to Article 32.2., only those original names have to be corrected which are listed in Article 32.5. A reference to cases like "*doriae*" is not listed. Therefore, I am using the name as it is originally published.

Jeannel (1957), who still regarded all species of *Syleter* from the Oriental and Ethiopian region in one genus, provided an ink sketch of the male aedeagus from a *S. doriae* specimen from Sumatra. However, the drawing more resembles to the aedeagus of a *S. paradoxus* specimen (Jeannel, 1957, p. 138, fig. 8).

***Parasyleter porphyreus* (Andrewes, 1923)**

Figs 3, 11, 17, 20

Psilus porphyreus Andrewes, 1923: 227. – Andrewes, 1927: 267. – Andrewes, 1928: 178. – Andrewes, 1929: 389. – Andrewes, 1930: 288.

Psilus porphyreus. – Csiki, 1927: 496.

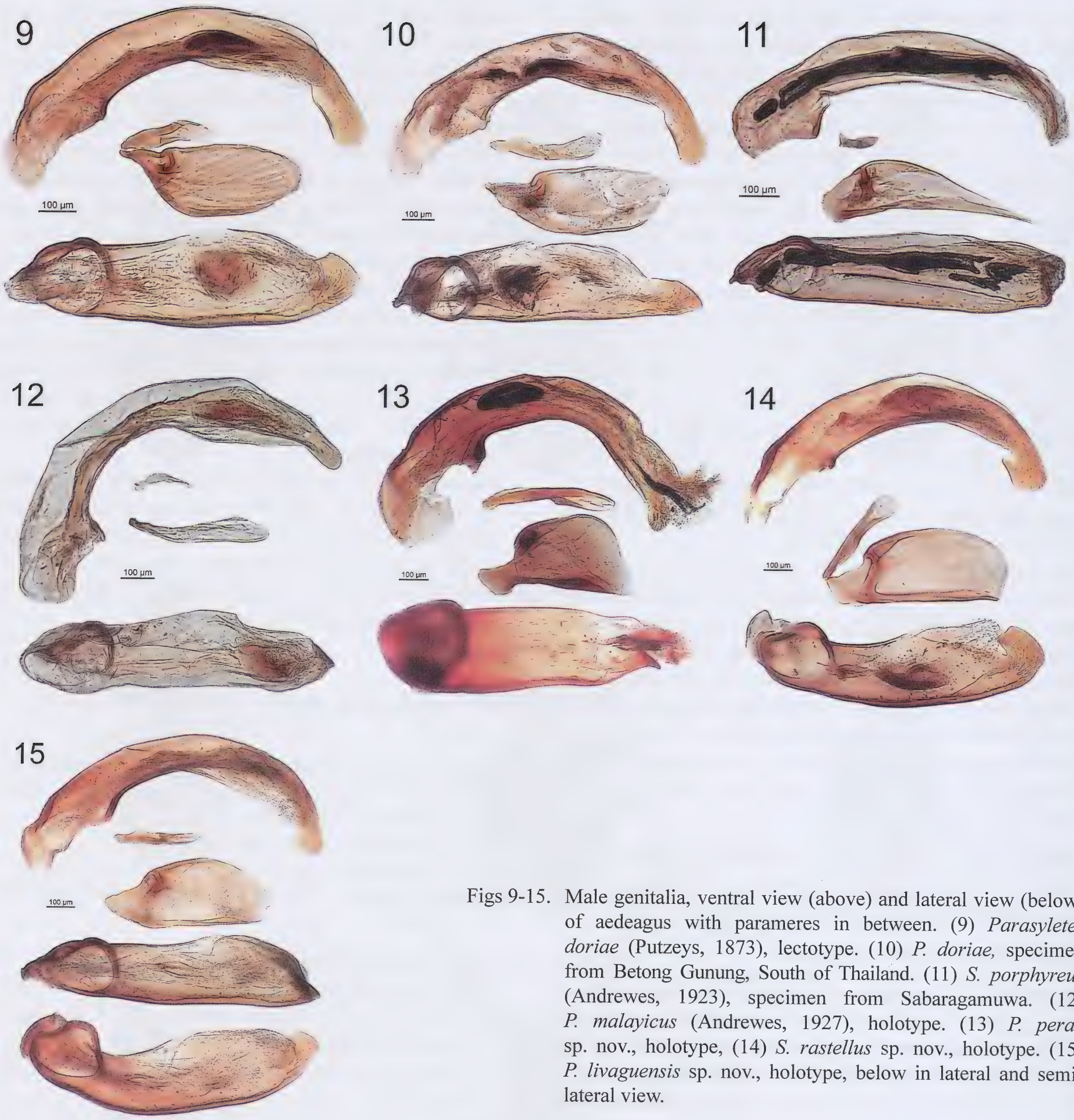
Syleter porphyreus. – Lorenz, 1998: 138. – Lorenz, 2005: 148.

Syleter porphyreus. – Balkenohl, 2001: 30. – Balkenohl, 2021: 369.

Type material examined: *Holotype*: BMNH; ♀, with labels and data: white, handwritten in black ink "Kotte Ceylon 4-IV-21" / Ceylon 1922 . 215" / handwritten and printed in black ink "Psilus porphyreus Andr. Type H.E.Andrewes det." / circle, red framed, black printed "Type H.T.".

Additional material: MNHN; 1 ♀, Galle E. Simon 1892 / MUSEUM PARIS Ex Coll. M. MAINDRON Coll. G. BABAULT 1930 / handwritten Clivina fulvaster Mots. – NHMG; 2 ♂, 2 ♀, 1 spec., CEYLAN Sabaragamuwa Ratanapura 21.I.70 MUSSARD BESUCHET LÖBL. – MNHN; 1 ♀, Colombo Simon 1892 / MUSEUM PARIS Ex Coll. M. MAINDRON Coll. G. BABAULT 1930. – MFNB; 4 specs., Ceylon Nietner / 4153 / Zool- Mus. Berlin.

Extended diagnosis: *Head* anterior eyes conspicuously elongated, with impressed straight transverse clypeal furrow, clypeus completely covered with isodiametric reticulation, fused with clypeal wings, straight anteriorly, laterally slightly more projecting as clypeus; supraantennal plates keeled, smooth, frontal furrows



Figs 9-15. Male genitalia, ventral view (above) and lateral view (below) of aedeagus with parameres in between. (9) *Parasyleter doriae* (Putzeys, 1873), lectotype. (10) *P. doriae,* specimen from Betong Gunung, South of Thailand. (11) *S. porphyreus* (Andrewes, 1923), specimen from Sabaragamuwa. (12) *P. malayicus* (Andrewes, 1927), holotype. (13) *P. perak* sp. nov., holotype, (14) *S. rastellus* sp. nov., holotype. (15) *P. livaguensis* sp. nov., holotype, below in lateral and semi-lateral view.

deep, frons isodiametrically reticulated, supraorbital furrows wide, distinctly diverging posteriorly; neck constriction visible laterally as row of few punctures, with wide gap at middle; labrum slightly concave, seven-setose; mandible distinctly elongated; eye convex, of regular size in lateral view, somewhat flattened in dorsal view; gena small. *Pronotum* sub-trapezoid, convex, as wide as long, slightly narrowed in anterior half; reflexed lateral margin ending at posterior setigerous puncture; posterior angle completely rounded off; flange convex, two times as wide as basal constriction; disk smooth, median line narrow, joining with anterior transverse line and finely with basal constriction. *Elytron* elongated, more than 1.5 times longer than wide, with nearly straight margin anterior at middle, maximum width at middle; humerus distinct, reflexed lateral margin smooth, with small humeral tooth, interval eight slightly wider than seven; striae distinctly punctate-striate; lateral channel somewhat narrower at middle, row of umbilical setigerous punctures with small gap at middle; lateral margin at apex conspicuously widened by emargination of interval eight. *Hind wings* well developed. *Legs* with protarsomeres slightly widened in both sexes. *Male genitalia* (Fig. 11) with aedeagus in ventral view slightly curved in its whole length, distinctly curved directly at apex, at apex with distorted short and rounded lamella; in lateral view straight; parameres

asetose. *Female genitalia* (Fig. 17) with gonocoxite distinctly curved to apex, with small hook at apex; with moderately sized cone-like seta at beginning of apical third, ventro-medially with thirteen nematiform setae; laterotergite with four moderately long nematiform setae. *Measurements.* Body length 2.29-2.61 mm ($\bar{x}$: = 2.43 mm*), width 0.82-0.9 mm ($\bar{x}$: = 0.85 mm*), ratio length/width of pronotum 0.95-1.01 ($\bar{x}$: = 0.97*), ratio length/width of elytra 1.53-1.55 ($\bar{x}$: = 1.54*); (*n = 10).
Variability: The median line of the pronotum is just not joining the basal constriction in the holotype. In some of the other material it finely joins the basal constriction.

Distribution: Southwest of Sri Lanka (Fig. 20).

Type locality: Kotte, Sri Lanka.

Remark: Andrewes (1923) described and redescribed (1929) the species. The description is based on the single holotype.

***Parasyleter malayicus* (Andrewes, 1927)**
Figs 4, 12, 20

Psilus malayicus Andrewes, 1927: 267. – Andrewes, 1930: 288.
Psilus malayicus. – Csiki, 1933: 638.
Syleter malayicus. – Lorenz, 1998: 138. – Lorenz, 2005: 148.
Syleter malayicus. – Balkenohl, 2001: 30. – Balkenohl, 2021: 369.

Type material examined: *Holotype*: BMNH; ♂, with labels and data: white, printed in black, yellow underlined and handwritten "Penang, G.E.Bryant. X 1913." / red, printed "Type" / white, handwritten and printed "Psilus malayicus Type Andr. H.E.Andrewes det." / "H.E.Andrewes Coll. B.M.1945-97.".

Extended diagnosis: *Head* anterior eyes distinctly elongated, with distinctly impressed straight transverse clypeal furrow; clypeal field at middle sub-rectangular, separated from wide frontal furrows by carinae, with distinct regular isodiametric reticulation, clypeal wing with irregular reticulation, slightly projecting anteriorly; supraantennal plate nearly smooth, keeled posteriorly up to end of gena-level; frons with fine not very regular isodiametric reticulation, laterally with elongated tubercle; neck constriction not visible; labrum concave, seven-setose; mandible distinctly elongated; eye conspicuously reduced, shape circular, directed antero-laterally, surrounded by dark pigment, pointed anteriorly; gena two times as long as eye, as high as eye. *Pronotum* sub-trapezoid, slightly wider than long, slightly narrowed in anterior half, posterior angle obtuse, just traceable; reflexed lateral margin just running over posterior setigerous puncture; basal constriction narrow, flange convex, two times as wide as basal constriction; disk smooth, median line narrow, joining with anterior transverse line, just not joining basal constriction. *Elytron* oval, 1.4 times longer than wide, maximum width at middle; reflexed lateral margin nearly smooth, sub-serrulate, humeral tooth small, just visible, situated posteriorly, slightly convex; interval eight as wide as seventh; striae distinctly punctate, punctures slightly to moderately impressed, distinctly shortened to base, stria one reaching apex, all others shortened apically; lateral channel with umbilical setigerous punctures of equal distance; lateral margin at apex conspicuously widened by emargination of interval eight. *Hind wings* not visible. *Legs* with protarsomeres slightly widened. *Male genitalia* (Fig. 12) with aedeagus in ventral view distinctly curved in basal two-thirds, thickened in apical third, at apex with elongated distorted spatula; in lateral view nearly straight; parameres small, asetose. *Female genitalia* unknown. *Measurements.* Body length 1.92 mm, width 0.74, ratio length/width of pronotum 0.92, ratio length/width of elytra 1.41.
Variability: Unknown.

Distribution: Known from the type locality, the island of Penang in West Malaysia (Fig. 20).

Type locality: Penang, West Malaysia.

Remark: According to the description, there is no other type material available. The species is well described by Andrewes (1927).

***Parasyleter perak* sp. nov.**
Figs 5, 13, 20

Holotype: NHMG; ♂, with labels and data: white, black printed and handwritten "MALAISIE Perak Maxwell Hill T. Jaccoud 8. IX. 72", backside handwritten " Mal-72/9" / white, printed " Syleter nr. malayicus ANDR. det. Balkenohl X.94".

Paratype: MBCB; ♂, same data as holotype.

Diagnosis: A small sized species with five-setose labrum, the clypeus and frons isodiametrically reticulated, and distinctly reduced eyes. Differentiated mainly from the other two species with reduced eyes (*P. malayicus* and *P. kerdil* sp. nov.) by the conspicuously square pronotum, and the shape of the eyes which are long-ovoid dorso-ventrally.

Etymology: The name is a noun and refers to the type locality of the species, Perak in West Malaysia.

Description:
Measurements: Body length 2.11 / 2.18 mm, width 0.81 / 0.81 mm, ratio length/width of pronotum 0.91 / 0.90, ratio length/width of elytra 1.46 / 1.45.
Colour: Piceous, with rufous tinge. Antenna, palpi, and legs flavous. Supraantennal plate and wing of clypeus translucent laterally.
Head: Distinctly narrower than a third of pronotum, frons and clypeus anterior eye-level distinctly elongated.

Clypeus indistinctly convex anteriorly, with lateral angle obtuse rounded and slightly projecting, fused with clypeal wing and supraantennal plate, all reflexed margined, clypeus flattened, separated from elongated convex supraantennal plate by parallel running deep and wide clypeal furrows, extending up to anterior eye-level; supraantennal plate keeled, extended over eye-level to posterior end of gena-level; clypeus separated from frons by a distinct transverse furrow. Frons slightly convex, supraorbital furrow wide. Clypeal, frontal, and supraorbital furrow connected. Clypeus and frons with indistinct isodiametric reticulation; supraantennal plate smooth, with small depression posteriorly. Neck with slight constriction laterally. Eye conspicuously reduced, shape long-ovoid dorso-ventrally in lateral view, surrounded by dark pigment, directed anterio-laterally, gena one and a half times as long as eye, about as high as eye. Antenna reaching distinctly over posterior setigerous puncture of pronotum, antennomeres five to ten elongated (around 1.4 times longer than wide). Labrum distinctly convex anteriorly, irregularly reticulated, five-setose, the central and the two lateral setae robust, the intermediate ones indistinct.

Pronotum: Disk in lateral view slightly convex, moderately convex in frontal view but slightly flattened laterally. Outline conspicuously square, slightly wider than long, widest at middle. Reflexed lateral margin smooth, running over posterior setigerous puncture by diameter of pore; anterior angle slightly projecting; posterior angle rounded off. Lateral channel narrow, as wide as reflexed lateral margin, marginal setigerous punctures located in the channel. Median line narrow, anteriorly evanescent, not joining anterior transverse line, joining indistinctly basal constriction; anterior transverse line wider than median line. Surface smooth, laterally with indistinct irregular reticulation; basal constriction narrow, flange short.

Elytron: Disk regularly convex in lateral and frontal view. Oval, around 1.5 times longer than wide, maximum width at middle. Reflexed lateral margin subserrulated, humeral tooth sharp, small, situated posteriorly; intervals slightly convex, eighth as wide as seventh; striae punctate-striate, punctures slightly to moderately impressed, shortened at base, stria one reaching apex, all others shortened apically; lateral channel with umbilical setigerous punctures of equal distance; lateral margin at apex conspicuously widened by emargination of interval eight.

Hind wings: Not visible.

Dorsal surface: Proepisternum smooth. Sternites of abdomen slightly transversely sulcate, smooth.

Legs: Protibia sulcate, smooth, with apical spine moderately arcuate, the two lateral spines obtuse and small, movable spur regularly arcuate.

Male genitalia (Fig. 13): Aedeagus in ventral view with long basal opening, distinctly curved at middle by about 110°, at apex with short, turned and distorted spatula, in lateral view nearly straight, apical tip turned dorsally; dorsal paramere elongated, ventral one wide, both asetose.

Female genitalia: Unknown.

Variability: In the paratype, the clypeal field is somewhat depressed.

Distribution: Known from the type locality Perak in West Malaysia (Fig. 20).

Parasyleter kerdil sp. nov.

Figs 6, 18, 20

Holotype: SMNS; ♀, with labels and data: white, black printed "W-MALAYSIA: Lake Kenyir, 5 km SW dam, 50 km SW Kuala Terengganu, ~350 m, 7.-12.VII.2001, leg. A.SCHULZ & K.VOCK".

Diagnosis: A very small sized species with five-setose labrum, the clypeus and frons isodiametrically reticulated, and distinctly reduced eyes. Differentiated mainly from the other two species with reduced eyes (*P. malayicus* and *P. perak* sp. nov.) by the very small body size, and the elytra with flattened intervals, less impressed and apically shortened punctures and striae. Moreover it is the only species with striae one and two free at the base of the elytron.

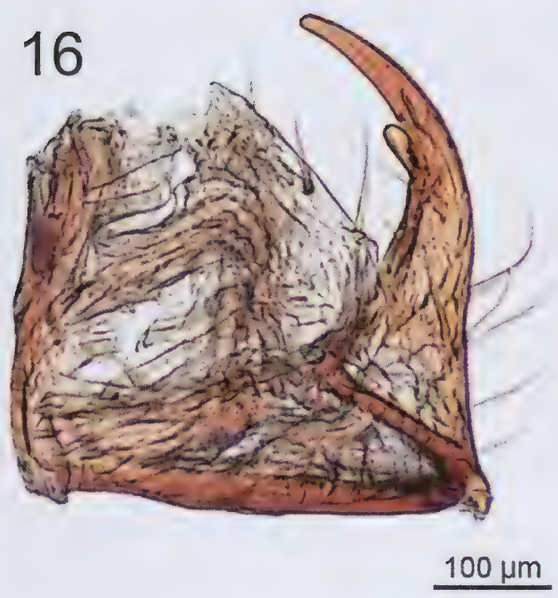
Etymology: The name is a noun and derived from the Malaysian language. The masculine word for dwarf is Kerdil and refers to the very small body size of the species.

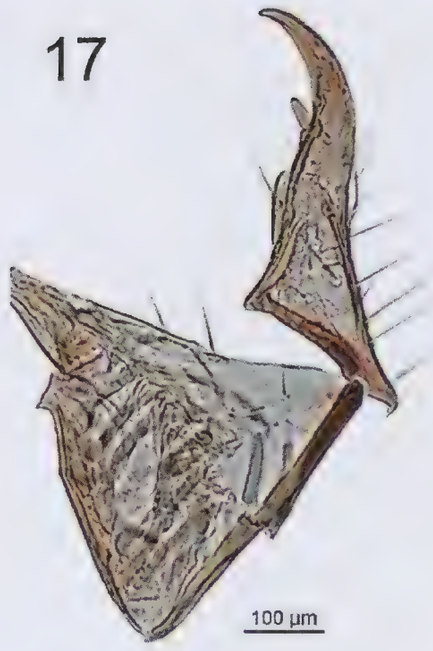
Description:

Measurements: Body length 1.8 mm, width 0.66 mm, ratio length/width of pronotum 0.86, ratio length/width of elytra 1.51.

Colour: Testaceous to rufous. Antenna, palpi, and legs flavous. Supraantennal plate and wing of clypeus translucent laterally.

Head: Distinctly narrower than a third of pronotum, frons and clypeus anterior eye-level distinctly elongated. Clypeus slightly convex anteriorly, with lateral angle obtuse rounded, fused with clypeal wing and supraantennal plate, all reflexed margined, clypeus with U-shaped blunt carina, slightly hollowed out at middle, separated from elongated convex supraantennal plate by parallel running deep and wide clypeal furrows, extending up to eye-level; supraantennal plate keeled, extended over eye-level to posterior end of gena-level; clypeus separated from frons by the bottom of the U-shaped carina. Frons slightly convex, supraorbital furrow wide. Clypeal and supraorbital furrow connected. Clypeus, frons and supraantennal plate with indistinct isodiametric reticulation; supraantennal plate with longitudinal depression posteriorly. Neck constriction not present. Eye conspicuously reduced, convex, nearly circular in lateral view, surrounded by dark pigment,





Figs 16-19. Female gonocoxites with laterotergite. (16) *Parasyleter doriae* (Putzeys, 1873), specimen from Sarawak. (17) *P. porphyreus* (Andrewes, 1923), holotype. (18) *P. kerdil* sp. nov., holotype. (19) *P. rastellus* sp. nov., paratype.

projecting distinctly anteriorly, gena two and a half times as long as eye, about as high as eye. Antenna reaching distinctly over posterior setigerous puncture of pronotum, antennomeres five to ten elongated (around 1.5 times longer than wide). Labrum distinctly convex anteriorly, irregularly reticulated, five-setose.

Pronotum: Disk in lateral view slightly convex, moderately convex in frontal view. Outline sub-trapezoid, wider than long, widest in posterior third. Reflexed lateral margin smooth, running over posterior setigerous puncture by two diameters of pore; anterior angle slightly projecting; posterior angle rounded off. Lateral channel narrow, as wide as reflexed lateral margin, marginal setigerous punctures located in the channel. Median line narrow, joining anterior transverse line, finely approaching basal constriction; anterior transverse line wider than median line. Surface smooth; basal constriction narrow, flange short.

Elytron: Disk regularly convex in lateral and frontal view, slightly flattened at sutura in frontal view. Oval, a third longer than wide, maximum width at middle. Reflexed lateral margin subserrulated, humeral tooth small but distinct, situated posteriorly; intervals smooth, flattened, eighth wider than seventh, striae one and two free at base, striae almost punctate-striate, punctures of striae slightly impressed, evanescent, striae shortened at base, one reaching apex, all others obsolete in apical quarter, lateral channel narrower at middle, umbilical setigerous punctures with gap at middle; lateral margin at apex conspicuously widened by emargination of interval eight.

Hind wings: Not visible.

Dorsal surface: Proepisternum indistinctly reticulated. Sternites of abdomen slightly transversely sulcate, smooth.

Legs: Protibia slightly sulcate, with fine longitudinal reticulation, with apical spine distinctly arcuate, the basal lateral spine obtuse, the other much larger and acute, movable spur regularly arcuate.

Male genitalia: Unknown.

Female genitalia (Fig. 18): Gonocoxites not much sclerotized, straight in basal three-quarters, gently curved apically, with small cone-like seta before beginning of apical quarter, ventro-medially with eight nematiform setae; laterotergite with three moderately long nematiform setae.

Variability: Unknown.

Distribution: Known from the type locality, Lake Kenyir in West Malaysia (Fig. 20).

***Parasyleter rastellus* sp. nov.**

Figs 7, 14, 19, 20

Holotype: RBINS; ♂, with labels and data: yellow, black printed "CAMBODIA Siem Reap, Angkor Thom 26.V.2003 Light trap Leg. J. Constant, K. Smets & P. Grootaert Coll. I.R.Sc.N.B. (RBINS)".

Paratypes: MHNG; 1 ♂, 1 ♀, VENTIANE [sic] LAOS. 64. R / Coll. J. Ochs in Coll. M. Curti MHNG-1991. – PBCP; 1 ♂, 1 ♀, 2 specs., VIETNAM Nat. park NAM CAT TIEN 1. – 15. 5. 1994 Zacharda lgt.

Diagnosis: A large-sized species with five-setose labrum, the clypeus isodiametrically reticulated and the frons smooth, and fully developed eyes. Differentiated mainly from *P. porphyreus* by the five-setose labrum and the smooth frons of the head. Differentiated mainly from *S. doriae* by the elevated smooth clypeal field. Moreover, the species is extraordinary characterized from all other species by the peculiar apex of the male aedeagus.

Etymology: The name is a noun and refers to the apex of the male aedeagus (Latin rastellus, masculine = small hoe).

Description:
Measurements: Body length 2.25-2.44 mm ($\bar{x}$: = 2.35 mm*), width 0.78-0.85 mm ($\bar{x}$: = 0.82 mm*), ratio length/width of pronotum 0.89-0.91 ($\bar{x}$: = 0.9*), ratio length/width of elytra 1.55-1.63 ($\bar{x}$: = 1.6*); (*n = 7).
Colour: Piceous. Antenna, palpi, and legs testaceous. Supraantennal plate translucent laterally.
Head: Distinctly narrower than a third of pronotum, frons and clypeus anterior eye-level conspicuously elongated. Clypeus straight anteriorly, with lateral angle obtuse rounded, fused with clypeal wing and supraantennal plate, all reflexed margined, clypeal field elevated, square, flattened, smooth, separated from anterior margin of clypeus by flat distinctly isodiametrically reticulated area, separated from frons by a distinct straight transverse furrow, separated from elongated convex supraantennal plate by parallel running deep and wide clypeal furrows, extending up to anterior eye-level; supraantennal plate keeled posteriorly, extended over eye-level to posterior end of gena-level; clypeus separated from anterior margin by flat isodiametrically reticulated area, clypeus separated from frons by a distinct transverse furrow. Frons slightly convex, smooth, supraorbital furrow wide. Clypeal, frontal, and supraorbital furrow connected. Frons with slight central pore at middle, laterally with obtuse carina. Neck constriction not developed, with few punctures laterally. Eye convex, of regular size in lateral view, somewhat flattened in dorsal view, gena indistinct. Antenna reaching up to base of pronotum, antennomeres five to ten elongated (around 25% longer than wide). Labrum straight anteriorly, indistinctly reticulated, five-setose, the central and the two lateral setae robust, the intermediate ones indistinct.
Pronotum: Disk in lateral view slightly convex, regularly convex in frontal view but slightly impressed at median line. Outline sub-trapezoid, convex to globose, wider than long, widest in posterior third, narrowed in anterior half, posterior angle completely rounded off. Reflexed lateral margin smooth, ending in posterior setigerous puncture; anterior angle not projecting. Lateral channel narrow, as wide as reflexed lateral margin, anterior marginal setigerous puncture removed from channel by diameter of pore, posterior puncture located in the channel. Median line narrow but distinct in its whole length, joining anterior transverse line; anterior transverse line wider than median line, consisting of row of punctures. Surface smooth, with indistinct transverse rugae; basal constriction distinct, flange about 1.5 as wide as constriction.
Elytron: Disk flattened in anterior half in lateral view, regularly convex in frontal view. Elongated, around 1.6 times longer than wide, with nearly straight but slightly diverging margin anterior middle, maximum width posterior middle. Humerus distinct. Apex pointed. Reflexed lateral margin subserrulated, humeral tooth small but visible, situated just posterior to humerus; intervals smooth, moderately convex, eighth as wide as seventh and at apex with carina-like concave vault; striae punctate-striate, punctures distinctly impressed, stria one reaching apex, two to seven ending before reaching apex at carina-like vault of interval eight; lateral channel with umbilical setigerous punctures narrower at middle, at apex conspicuously widened by emargination of interval eight.
Hind wings: Fully developed.
Dorsal surface: Proepisternum smooth. Sternites of abdomen slightly transversely sulcate, terminal sternite at apex with indistinct punctured reticulation in males, half of sternite covered with distinct reticulation in females.
Legs: Protibia sulcate, with indistinct longitudinal reticulation, with apical spine distinctly arcuate, the two lateral spines obtuse, movable spur regularly arcuate.
Male genitalia (Fig. 14): Aedeagus in ventral view with long basal opening, moderately and regularly curved, at apex with short flattened but conspicuous hoe; in lateral view nearly straight, apical tip distorted, turned ventrally; internal sac with five large triangular teeth; ventral paramere wide, both parameres rounded at apex, both asetose.
Female genitalia (Fig. 19): Gonocoxites regularly curved, slender in apical half, base stout, with moderately sized cone-like seta at middle, ventro-medially with nine long nematiform setae; laterotergite with two long and one short nematiform setae.
Variability: In two of the paratypes, the clypeal field is somewhat unevenly structured. The median pore on the frons of the head is more or less impressed.

Distribution: From the South of Laos over Cambodia to the South of Vietnam (Fig. 20).

***Parasyleter livaguensis* sp. nov.**
Figs 8, 15, 20

Holotype: BMNH; ♂, with labels and data: white, handwritten in black ink, with first line underlined in yellow "6. SABAH Mt. Kinabalu Nat. Pk. 5000 Ft R. Livagu 9. VIII. 1982 N.E. Stork B.n. 1982 – 388" / printed and handwritten "river bank debris Gravel area".

Paratype: MBCB; ♂, MALAYSIA-Sabah Kinabatangan river near village Kg. Koyah 4.-5.6.98, J. Horák leg.

Diagnosis: A large-sized species with five-setose labrum and fully developed eyes. Different mainly from *S. porphyreus* by the five-setose labrum and the smooth frons of the head. Differentiated mainly from *S. doriae* and *S. rastellus* by the big eye and the narrowed lateral margin and channel of the pronotum. Moreover, it is the only species with a longitudinal group of small punctures laterally on the pronotum. In addition, the species is very characterized from all other species by the differences in the male aedeagus.

Fig. 20. Map of East Asia providing an overview on the occurrence of *Parasyleter* species described so far (recorded localities plotted). 1 (black) *P. doriae* (Putzeys, 1873); 2 (white) *P. porphyreus* (Andrewes, 1923); 3 (black circle) *P. malayicus* (Andrewes, 1927); 4 (red) *P. perak* sp. nov.; 5 (yellow) *P. kerdil* sp. nov.; 6 (blue) *P. rastellus* sp. nov.; 7 (orange) *P. livaguensis* sp. nov. Basic schematic map of Asia taken from SimpleMappr.net.

Etymology: The name is an adjective and refers to the river Livagu where the holotype was found.

Description:
Measurements: Body length 2.63/2.31 mm, width 0.86/0.85 mm, ratio length/width of pronotum 0.86/0.86, ratio length/width of elytra 1.6/1.58.
Colour: Testaceous. Antenna, palpi, and clypeal field flavous. Supraantennal plate translucent laterally.
Head: Distinctly narrower than a third of pronotum, frons and clypeus anterior to the eye-level conspicuously elongated. Clypeus indistinctly convex anteriorly, with lateral angle distinct but rounded, fused with clypeal wing and nearly completely with supraantennal plate, all reflexed margined, clypeal field slightly elevated, square, with flattened and slightly uneven surface, separated from elongated convex supraantennal plate by slightly diverging wide clypeal furrows, extending up to anterior eye-level; supraantennal plate keeled posteriorly, extended over eye-level to posterior end of gena-level, clypeal field separated from anterior margin of clypeus by flat irregular reticulated area, clypeal field separated from frons by a distinct straight transverse furrow. Frons slightly convex, smooth, supraorbital furrow moderately wide, deep. Clypeal, frontal, and supraorbital furrows connected. Frons without central pore, laterally with indistinct carina. Neck constriction not developed. Eye relatively large, nearly hemispherical, projecting laterally, surrounded by dark pigment, gena indistinct. Antenna reaching up to base of pronotum, antennomeres five to ten elongated (around 40% longer than wide). Labrum concave anteriorly, indistinctly reticulated, five-setose, the central and the two lateral setae longer than the intermediate ones.
Pronotum: Disk in lateral view slightly convex, regularly convex in frontal view but distinctly impressed at median line. Outline sub-trapezoid, transverse, widest before posterior setigerous punctures, narrowed convex in anterior half, posterior angle indistinctly indicated by a slight thickening of the marginal margin. Reflexed lateral margin smooth, narrower at middle, extended over posterior setigerous puncture by one to two diameters of pore; anterior angle not projecting, rounded off. Lateral channel narrower at middle, marginal setigerous punctures located nearly in the channel. Median line deep, consisting of irregularly joining longitudinal punctures, joining anterior transverse line; anterior transverse line slightly wider than median line, consisting of row of punctures. Surface smooth, laterally with longitudinal group of small punctures; basal constriction distinct, flange more than 1.5 wider than constriction.
Elytron: Disk slightly convex in anterior half in lateral view, regularly convex in frontal view, flattened at sutura and first interval. Elongated, around 1.6 times longer than wide, with short straight but diverging part anterior middle, maximum width posterior middle. Humerus distinct. Apex slightly pointed. Reflexed lateral margin slightly subserrulated in anterior half, serrulation partly nearly invisible, more distinct posteriorly, humeral tooth small but sharp, situated just posterior to humerus; intervals smooth, moderately convex, first flattened in anterior half, eighth wider than seventh and at apex with carina-like concave vault; striae punctate-striate, punctures distinctly impressed, stria one reaching apex, two to seven ending before reaching apex at carina-like vault of interval eight; lateral channel with umbilical setigerous punctures narrower at middle, at apex conspicuously widened by emargination of interval eight.
Hind wings: Wings developed.
Dorsal surface: Proepisternum with fine transverse rugae, nearly smooth. Sternites of abdomen slightly transversely sulcate, terminal sternite in apical third with indistinct meshed reticulation (male).
Legs: Protibia nearly smooth, with apical spine moderately arcuate, the two lateral spines distinct, movable spur thin, slightly arcuate.
Male genitalia (Fig. 15): Aedeagus in ventral view with long basal opening, moderately and regularly curved, at apex with moderately sized flattened and distorted spatula; in lateral view straight, with flattened lateral side; internal sac with small group of fine bristles at middle; ventral paramere wide, both parameres somewhat acuminated at apex, both asetose.
Female genitalia: Unknown.
Variability: In the paratype the eyes are slightly less convex compared to the holotype.

Distribution: Known from the type locality in the Mount Kinabalu National Park at the rivers Liwagu [Livagu river] and Kinabatangan in Sabah, Malaysia Borneo (Fig. 20).

Specimen incertae sedis

BMNH; 1 ♀, blue, handwritten in black ink "Siam" / white, printed "Bowring 63.47*". *Remark*: The specimen was submitted without head and pronotum.

DISCUSSION AND CONCLUDING NOTES

So far, the genus *Parasyleter* has been recorded from Thailand, Cambodia, the South of Vietnam, and over the Malay Archipelago up to the Wallace Line. In addition, it occurs in Sri Lanka (Fig. 20).
Four of the seven species were found on the Malay Peninsula with three of them with peculiar adaptations such as evidently reduced eyes, distinctly enlarged genae, a serrulated lateral margin of the elytra, oval shape of the elytra without humeri, missing hind wings, and uniformly brown colour. These combination of characters are considered as adaptations to deeper layers in the soil. Such characters are usually found in species with reduced dispersal power. Therefore, it is hypothesized that these species are endemic on the Malayan peninsula.

Out of the three species with these conspicuous adaptations (*P. malayicus, perak* sp. nov., *kerdil* sp. nov.), *P. kerdil* sp. nov. exhibits the smallest eyes. In *P. doriae* the eyes are not distinctly reduced but somewhat flattened. In addition, specimens from Borneo seem to have slightly less elongated elytra. Some specimens from Borneo show reduced hind wings. This character was not observed in specimens from West Malaysia. It is hypothesized that wing dimorphism is present in some populations of this species.

Parasyleter porphyreus from Sri Lanka seems to be not only geographically isolated. It is the only species with a seven-setose labrum and smooth lateral margin of the elytra.

However, zoogeographic considerations cannot be taken into account at present due to the very limited material available.

ACKNOWLEDGEMENTS

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Phylogeny and taxonomy of the African frog genus *Strongylopus* (Anura: Pyxicephalidae)

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Abstract: We present a molecular phylogeny of African stream frogs (genus *Strongylopus*), based on 12S rRNA, 16S rRNA, the nuclear recombination activating gene 1 (*RAG-1*) and tyrosinase exon 1 (*tyr*). Molecular data were supported by advertisement call analysis and morphology. We recognise six valid species: *Strongylopus bonaespei* (Dubois, 1981) from the southern and southwestern parts of the Western Cape Province, South Africa; *Strongylopus fasciatus* (Smith, 1849) from eastern South Africa to Zimbabwe; *Strongylopus grayii* (Smith, 1849) found throughout South Africa with older records in Naukluft, in central Namibia; *Strongylopus rhodesianus* (Hewitt, 1933) known from the eastern highlands of Zimbabwe and western Mozambique; *Strongylopus wageri* (Wager, 1961) from KwaZulu-Natal Province, South Africa and *Strongylopus merumontanus* (Lönnberg, 1907) from eastern Zambia, Malawi, northern Mozambique and Tanzania. *Strongylopus fuelleborni* (Nieden, 1911), *S. kitumbeine* Channing & Davenport, 2002 and *S. kilimanjaro* Clarke & Poynton, 2005 were shown to be junior synonyms of *Strongylopus merumontanus*. *Strongylopus springbokensis* Channing, 1986 is recovered as a junior synonym of *Strongylopus grayii*. Divergence ages were estimated, and discussed in terms of paleoclimatic events.

Keywords: Amphibia - Africa - phylogeny - integrative taxonomy - synonyms - advertisement calls - 12S rRNA - 16S rRNA - *tyr* - *RAG-1* - morphology - paleoclimate.

INTRODUCTION

Stream frogs in the genus *Strongylopus* are widespread in the south of Africa and at high elevations of tropical East Africa (Poynton, 2013), reaching low elevations only in the high latitudes. They are assigned to the endemic African family Pyxicephalidae (van der Meijden *et al.*, 2005), and presently 10 species are recognised (Frost, 2022).

Strongylopus bonaespei (Dubois, 1981), endemic to South Africa, is associated with the coastal lowlands and the higher mountainous regions running parallel with the Western Cape Province coast from west to east; *Strongylopus fasciatus* (Smith, 1849) is known from eastern South Africa to Mozambique, Zimbabwe, southern Zambia and the highlands of eastern Africa, including the Eastern Arc Mountains of Tanzania and the Nyika Plateau of Malawi; *Strongylopus fuelleborni* (Nieden, 1911) occurs on the isolated mountains in the south of Malawi and adjacent Mozambique; *Strongylopus grayii* (Smith, 1849) is widespread in South Africa at both lower and higher elevations, extending into Lesotho, and reaching the borders of Botswana in the north and an isolated population from Naukluft in central Namibia; *Strongylopus kilimanjaro* Clarke & Poynton, 2005 is only known from the high slopes (above 1700 m) of Mt. Kilimanjaro (Zancolli *et al.*, 2013); *Strongylopus kitumbeine* Channing & Davenport, 2002 is restricted to an extinct volcano, Mt. Kitumbeine in northern Tanzania; *Strongylopus merumontanus* (Lönnberg, 1907) similarly occurs on the highlands of an extinct volcano, Mt. Meru

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in northern Tanzania; *Strongylopus rhodesianus* (Hewitt, 1933) is known from the Eastern Highlands of Zimbabwe and the Gorongosa massif in western Mozambique; *Strongylopus springbokensis* Channing, 1986 is known from the arid area of Namaqualand in South Africa; *Strongylopus wageri* (Wager, 1961) is found on the uplands of KwaZulu-Natal Province, including the slopes of the Drakensberg.

The taxon has an unsettled taxonomic history and was regarded as a 'problematic' genus by Poynton (2013) due to the similarity of many of the species. *Strongylopus* was described by Tschudi in 1838, although it was still placed in the genus *Rana* by most workers for the next century. The status of the genus *Strongylopus* was later confirmed based on tadpole morphology (Van Dijk, 1966), but subsequently placed as a subgenus of *Rana* (Dubois, 1988). The misidentification of an *Amietia* gene sequence as *S. grayii* resulted in the apparent polyphyly of *Strongylopus* (Bittencourt-Silva *et al*., 2016; Channing *et al*., 2016). Presently the genus *Strongylopus* is recognised as part of the endemic African family Pyxicephalidae, which is not closely related to *Rana* (Channing, 2001; Frost *et al*., 2006; Channing *et al*., 2016; Du Preez & Carruthers, 2017). Frost (2022) presents a history of the taxonomic changes applied to *Strongylopus*, and there are still questions concerning the taxonomy of many of the species.

One problem is the occurrence of colour variations. For instance, a common colour pattern is longitudinal lines of black, brown and yellow, which may have caused confusion in the identification of *S. bonaespei, S. fasciatus* and the three northern species (Poynton, 1964b; Greig *et al*., 1979; Clarke & Poynton, 2005). Colour patterns may distinguish some species, although these can be very variable. Further pattern elements that vary include ventral spotting, vertebral stripes, and cross-banding on legs. Some morphological criteria are useful in species diagnosis, for example, *Strongylopus grayii* can be distinguished from *S. rhodesianus* by the ratio of head width/length of fourth toe (Poynton, 1964a). Morphological characters previously used to differentiate between taxa (Poynton, 1964a; Poynton & Broadley, 1985) include relative head width, relative snout length, relative diameter of tympanum, relative foot length, relative tibia length, and amount of webbing on the fourth toe. Advertisement calls are useful taxonomic characters in most instances (Passmore, 1977), as morphologically similar species of *Strongylopus* can be easily distinguished acoustically (Channing, 1979).

While most species have small distributions, *Strongylopus fasciatus* (Smith, 1849) and *S. grayii* (Smith, 1849) are widespread and expected to show some genetic sub-structure. *Strongylopus fuelleborni* is known from Tanzania, Malawi and northeastern Zambia. Loveridge placed *S. fuelleborni* as a synonym of *Rana fasciata merumontana* (1933), and later as a subspecies of *S. fasciata* (1953). Poynton (1964b) compared six specimens from each of six localities, and showed that the ratio of head width/foot length revealed three groups, one in South Africa and Zimbabwe (as *S. f. fasciatus*), one on Mt. Mulanje and Nyika Plateau (as *S. fasciatus fuelleborni*) and the third in the north on the Usambara and Poroto Mountains (as *S. fasciatus merumontana*). The proportions of the central *S. fuelleborni* are between those of the southern *S. fasciatus* and the northern *S. merumontanus*. *Strongylopus fuelleborni* which occurs on many isolated highlands (Conradie *et al*., 2018) was elevated to a full species by Channing (2001) based on advertisement call differences. Channing & Davenport (2002) based on similarity in advertisement calls and morphology, subsequently placed *S. fuelleborni* as a junior synonym of *S. merumontanus* (Lönnberg, 1907), which was described from Mt. Meru in northern Tanzania. Poynton (2004) regarded *S. merumontanus* as restricted to high elevations on Mt. Meru. Pickersgill (2007) used the name *S. fuelleborni* for the northern species as it was geographically separate from *S. fasciatus*. However, the integrity of this species has not been tested phylogenetically.

The other common species, the Clicking Stream Frog *Strongylopus grayii* (Smith, 1849) is widespread in South Africa, known from many vegetation types and a range of elevations. Tolley *et al*. (2010) showed differences between southwestern (winter rainfall) and northern (summer rainfall) populations, which they suggested might represent cryptic species. *Strongylopus kitumbeine* Channing & Davenport, 2002 was described from Mt. Kitumbeine, an extinct volcano in northern Tanzania. It was diagnosed based on some unique characters in morphology and advertisement calls. *Strongylopus kilimanjaro* Clarke & Poynton, 2005 is the most recently described species, distinguished on small morphological differences from *S. kitumbeine*. It is only known from Mt Kilimanjaro in Tanzania. *Strongylopus rhodesianus* (Hewitt, 1933) was originally described as a subspecies of *Rana grayi* (Hewitt, 1933). However, small samples of typical *S. grayii* and *S. rhodesianus* showed significant differences in the ratio of head length/length of fourth toe (Poynton, 1964a). *Strongylopus rhodesianus* is not well known, occurring on the Eastern Highlands of Zimbabwe and the adjacent highlands of Mozambique, including Mt Gorongosa. Poynton & Broadley (1985) thought it very likely that there was genetic mixing with *S. fasciatus*. *Strongylopus bonaespei* (Dubois, 1981) was originally described as *Rana fasciata montana* FitzSimons, 1946, and later named *Rana montana* by Greig *et al*. (1979). However, these names were preoccupied by *Rana temporaria* var. *montanus* Koch, 1872. The species was renamed *Rana* (*Strongylopus*) *bonaespei* by Dubois (1981). It occurs along the coast and on the mountains in the southern and southwestern Cape Province, South Africa. The little-known *Strongylopus springbokensis* Channing, 1986 occurs in the montane, arid region of Namaqualand in South Africa. *Strongylopus wageri*

(Wager, 1961) is known from the midlands of KwaZulu-Natal Province and the slopes of the Drakensberg Mountains in South Africa. Although the species was inadvertently described by Wager, there seem to be no taxonomic problems in this taxon (Poynton, 1963). In contrast the status of the taxa isolated on relatively small areas in northern Tanzania (*Strongylopus kitumbeine, S. kilimanjaro* and *S. merumontanus)* is in need of further study, i.e. to test their genetic isolation. Poynton (2004) showed that the northern *S. fuelleborni* is not related to the southern *S. fasciatus*. The early changes in nomenclature of these species are reviewed by Poynton (2013).
The purpose of this study is to re-evaluate the taxonomy of stream frogs, using nuclear and mitochondrial gene sequences, advertisement calls, and morphology.

MATERIALS AND METHODS

Sampling: The specimens used for the molecular study are listed in Appendix 1. This includes material from South Africa, Lesotho, Zimbabwe, Malawi, Mozambique, and Tanzania. Localities where advertisement calls were obtained are listed in Appendix 2. Finally, all material used for the morphological study is listed in Appendix 3.

Molecular: DNA extraction and amplification of fragments of mitochondrial 12S rRNA, 16S rRNA, the nuclear-coding tyrosinase exon 1 (*tyr*), and a fragment of the nuclear recombination activating gene 1 (*RAG-1*) followed standard protocols (Channing *et al*., 2016). We developed new nuclear recombination activating gene 1 (*RAG-1*) primers for *Strongylopus*, Rag1-Str-F1 (TGC TGC AAA CCC CTT TGC CTA) and Rag1-Str-R1 (TTC CCT TCG CTG GCC CA) and modified 12S primers: 12Sam F (TCCTRGCCTTRTCARCT) and 12Sam R (ATAGTGGGGTATCTAATCCCAGTTT). The annealing temperature for the *RAG-1* primers was 55°C, and 51°C for the 12Sam primers. Some samples were sequenced in both directions, and some were sequenced on two separate occasions. Sequences were aligned using Sequencher 5.4. GenBank sequences and sources are listed in Appendix 1. Uncorrected *p*-distances were calculated using PAUP* (Swofford, 2002). The uncorrected *p* distances for the mitochondrial 16S rRNA, nuclear *tyr* and *RAG-1* genes were compared between all available *Strongylopus* sequences. The genus *Amietia* is the appropriate outgroup for *Strongylopus* (Frost *et al.,* 2006; Jetz & Pyron, 2018, 2019). The outgroup sequence is a chimaera of *Amietia nutti* from Kenya (12S KU69367, 16S KU693777, *tyr* KU694111), and *Amietia delalandii* from Lesotho (*RAG-1* HQ014422).
The two most likely haplotypes for each individual for the nuclear genes were determined by first submitting the aligned sequences, including IUPAC polymorphism symbols, to SeqPhase step 1 (Flot, 2010), which produces an input file for PHASE (Stephens & Donnely, 2003). PHASE calculates the likelihood of possible haplotypes. The output is submitted to SeqPhase step 2, which produces full sequences for each haplotype (accessed at https://eeg-ebe.github.io/SeqPHASE). Haplotype networks for both nuclear gene fragments and the mitochondrial genes were determined using TCS 1.21 (Clement *et al.,* 2000) and illustrated using PopArt (Population Analysis with Reticulate Trees; http://popart.otago.ac.nz).
Phylogenies based on each gene separately (phased nuclear genes), and then on all four genes combined, for samples where this was possible, were generated using the Maximum Likelihood (ML) software IQ-TREE (Nguyen *et al.,* 2015; Trifinopoulos *et al.,* 2016). Aligned sequences were submitted to the website W-IQ-TREE (http://iqtree.cibiv.univie.ac.at). The ultrafast bootstrap UFBoot2 (Minh *et al.,* 2013; Hoang *et al.,* 2017) was determined using 1000 replicates. The software determined the appropriate model for the ML analysis: TIM2e+I+G4. Support values for the phylogeny were calculated as SH-aLRT (%) and the ultrafast bootstrap (%). The tree was rooted and drawn using FigTree 1.4.4 (Rambaut, 2018). Divergence dates for representatives of each species were estimated in BEAST 2.6.3 (Hasegawa *et al*., 1985; Heled & Drummond, 2012; Bouckaert *et al*., 2019), calibrating the tree based on a mean rate of change of 0.16% per million years for Pyxicephalidae 16S rRNA, after Bittencourt-Silva *et al*. (2016).

Museum acronyms: The museum acronyms used in the literature and their current equivalents follows Sabaj (2019). TMP – Transvaal Museum, Pretoria (now DNMNH – Ditsong National Museum of Natural History, Pretoria); BMNH – Natural History Museum, London; PEM – Port Elizabeth Museum, Bayworld complex, Gqeberha; NRM – Swedish Museum of Natural History, Stockholm; ZMB – Museum für Naturkunde, Leibniz Institute for Evolution- and Biodiversity Science, Berlin; CAS – California Academy of Sciences.

Advertisement calls: Most calls were obtained in the field using a Marantz PMD660 digital recorder with a directional microphone. Older recordings using a Sony cassette recorder were also included. Air temperature was noted. Call analysis was carried out using Raven Pro 1.6.1 (Center for Conservation Bioacoustics, 2019). Calls consist of brief clicks or whistles. Call parameters were determined following Köhler *et al*. (2017). The following call parameters were noted: dominant harmonic mid-point, other emphasised harmonics, pulses per note, note duration and note rate. Calls were classified into guilds following Emmrich *et al*. (2020).

Morphology: Measurements were taken with a digital calliper accurate to 0.01 mm, rounded to 0.1 mm, with the aid of a dissecting microscope. The following measurements were recorded: SUL – snout-urostyle length, HW – maximum head width, HL – head length measured from the back of the lower jaw to the snout tip,

SL – snout length measured form the anterior corner of the eye to the snout tip, EW – horizontal eye diameter, EN – distance between eye and nostril, ET – distance between eye and tympanum, TYM – horizontal tympanum diameter, FOT – foot length measured to include the inner metatarsal tubercle to the tip of the fourth toe, TIB – length of tibiafibula, HND – hand length, measured to include the palmar tubercle to the tip of the third finger. In addition, notes were made of ventral, snout, back and limb patterns. The dorsal vertebral skin ridges may be absent, interrupted or continuous, and this was noted. Colour patterns were scored from photos of live animals. The following ratios were calculated: HW/FOT – relative foot length as used by Poynton (1964a), SUL/HW – relative head width, SUL/SL – relative snout length, HW/EW – relative eye size, ET/EW relative distance between eye and tympanum, TYM/ET – relative tympanum size, SUL/TIB – relative tibiafibula length, TIB/FOT – relative foot to tibia length, HW/HND – relative hand length, SL/EW – snout length relative to eye width, FOT/SUL – length of foot relative to body length, EN/TYM – relative size of tympanum.

RESULTS

Molecular data

Phylogeny: The software proposed TIM2e + I + G4 as the appropriate model for the ML analysis. The phylogeny based on four genes showed six well-supported clades. The same topology was recovered from the four genes when analysed separately. We show the 16S and *tyr* trees as they included most samples (Figs 1, 2, 3). The 16S rRNA sequences (Figs 1, 2) show slight variation between the highland populations of *S. fuelleborni* on Mt. Mulanje (Malawi), *S. fuelleborni* on the Mt. Namuli and Mt. Mabu complex (Mozambique), *S. fuelleborni* at Nyanga and the highlands of eastern Zimbabwe, *S. fuelleborni* on the Mbizi Hill highlands south of Lake Rukwa in Tanzania, the Livingstone Mountains in Tanzania, and the Udzungwa Mountains in Tanzania, *S. kilimanjaro* on Mt. Kilimanjaro (Tanzania), *S. kitumbeine* on Mt. Kitumbeine (Tanzania) and *S. merumontanus* on Mt. Meru (Tanzania)(Fig. 4). The nuclear *tyr* phylogeny (Fig. 3) shows that many sequences of *S. kilimanjaro, S. fuelleborni*, *S. merumontanus* and *S. kitumbeine* are identical.

The 16S rRNA phylogeny (Fig. 2) shows that *S. springbokensis* sequences from Rooiberg and Studer Pass on the Namaqualand highlands are embedded within sequences of *S. grayii* from the southern and southwestern Cape in South Africa. Sequences of the nuclear *tyr* gene from the same localities (Fig. 3) places them basal to *S. grayii* but in a well-supported clade. *Strongylopus springbokensis* is thus regarded as a junior synonym of *S. grayii*.

Uncorrected p distances: The uncorrected *p* distances for 16S and the two nuclear genes, *tyr* and *RAG-1* are presented in Table 1. The uncorrected interspecific *p* distances for 16S varied from 2.8-7.4%, for *tyr* 0.2-3.6%, and for *RAG-1* 0.2-6.7%. The intraspecific uncorrected *p* distances for 16S varied from 0-2.1%, with the largest

Table 1. Range of uncorrected p-distances as percentages for 16S rRNA, *tyr* and *RAG-1* between *Strongylopus* taxa. GRA – *S. grayii*, FAS – *S. fasciatus*, MER – *S. merumontanus*, WAG – *S. wageri*, BON – *S. bonaespei*. RHO – *S. rhodesianus*. Top line –16S, middle line – tyrosinase exon 1, lowest line – *RAG-1*.

	GRA	FAS	MER	WAG	BON	RHO
GRA	0-1.7 0.2-1.0 0-0.8					
FAS	4.2-6.0 2.4-3.4 2.8-5.5	0-0.8 0-0.6 0-1.1				
MER	4.8-6.6 2.6-3.6 2.9-4.7	2.8-4.8 0.2-1.4 3.3-5.4	0-2.4 0-1.0 0-1.4			
WAG	4.8-5.6 2.4-3.0 2.7-4.2	5.6-6.3 2.8 3-6.7	6.0-7.4 3.0-3.3 3.3-5.0	0-0.2 0 0.7-1.5		
BON	4.4-5.8 1.8-2.8 2.7-3.9	5.0-5.4 2.2-3 3.3-6.4	2.8-6.4 2.4-3.4 3.3-4.3	5.8-5.9 2.4-3.0 2.4-3.8	0 0-0.6 0.4	
RHO	5.7-7.0 1.0-3.3 2.6-4.3	3.9-5.1 0.6-1.0 3.5-4.3	3.3-4.6 0.6-2.5 0.2-1.5	7.7 3.1 3.7-4.3	5.5-5.7 2.3-3.3 3.9-4.5	0 0 0-0.2

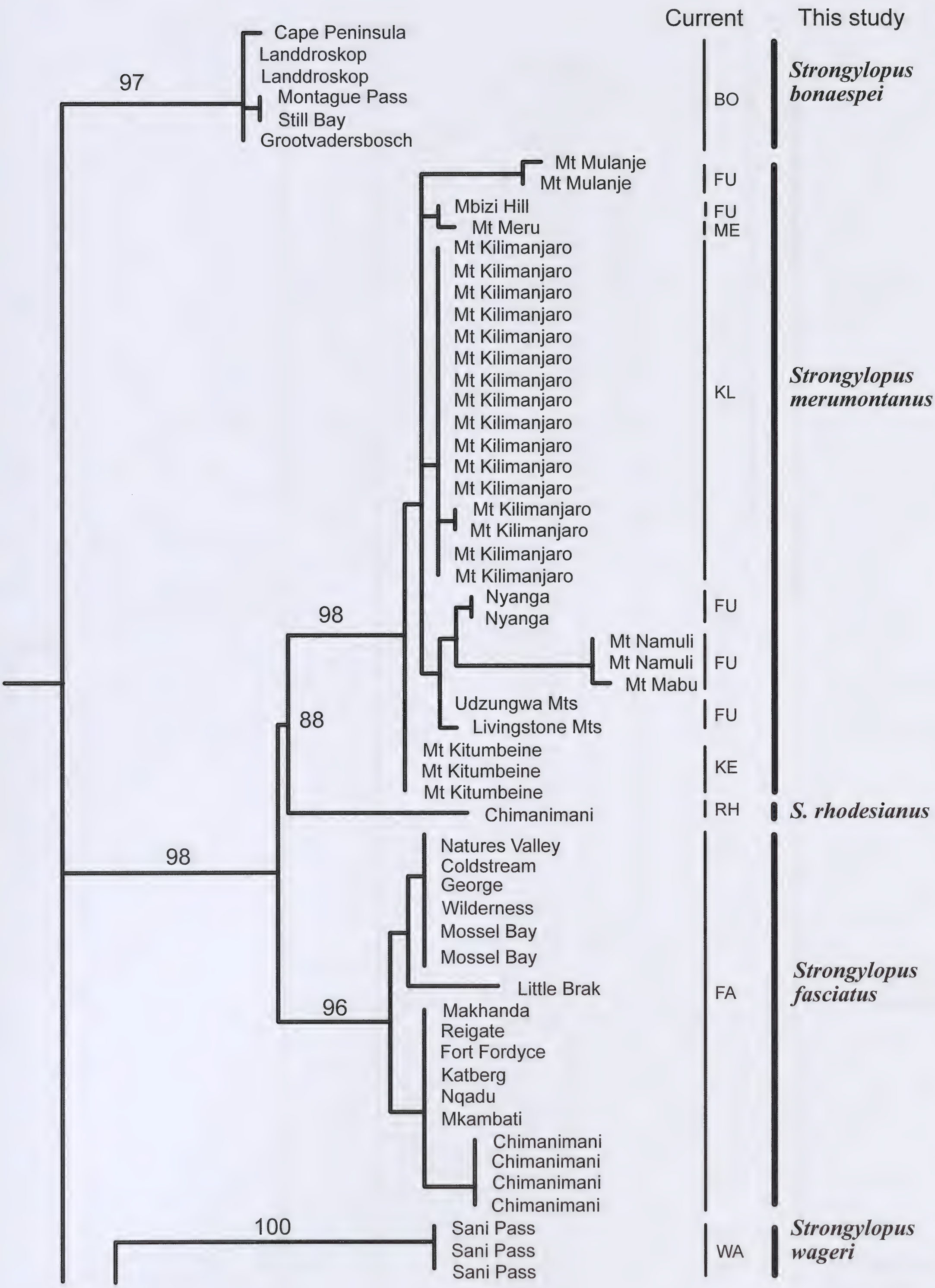

Fig. 1. Part 1 of Phylogeny of the genus *Strongylopus*, based on 16S rRNA. Current name codes: BO–*S. bonaespei*, FU–*S. fuelleborni*, ME – *S. merumontanus*, KL – *S. kilimanjaro*, KE – *S. kitumbeine*, RH – *S. rhodesianus*, FA – *S. fasciatus*, WA – *S. wageri*.

Fig. 1

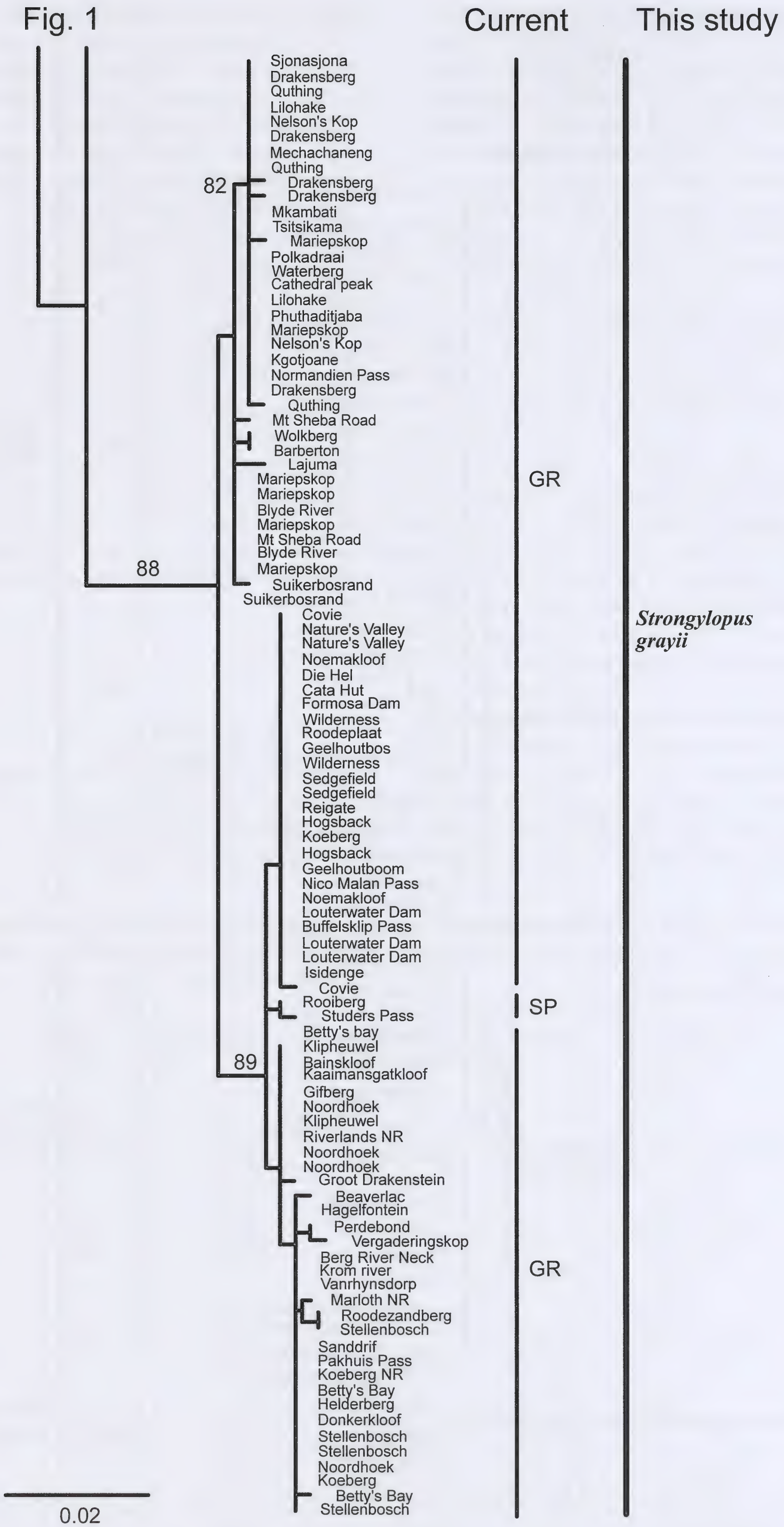

Fig. 2. Part 2 of Phylogeny of the genus *Strongylopus*, based on 16S rRNA. Current name codes: GR – *S. grayii*, SP – *S. springbokensis*.

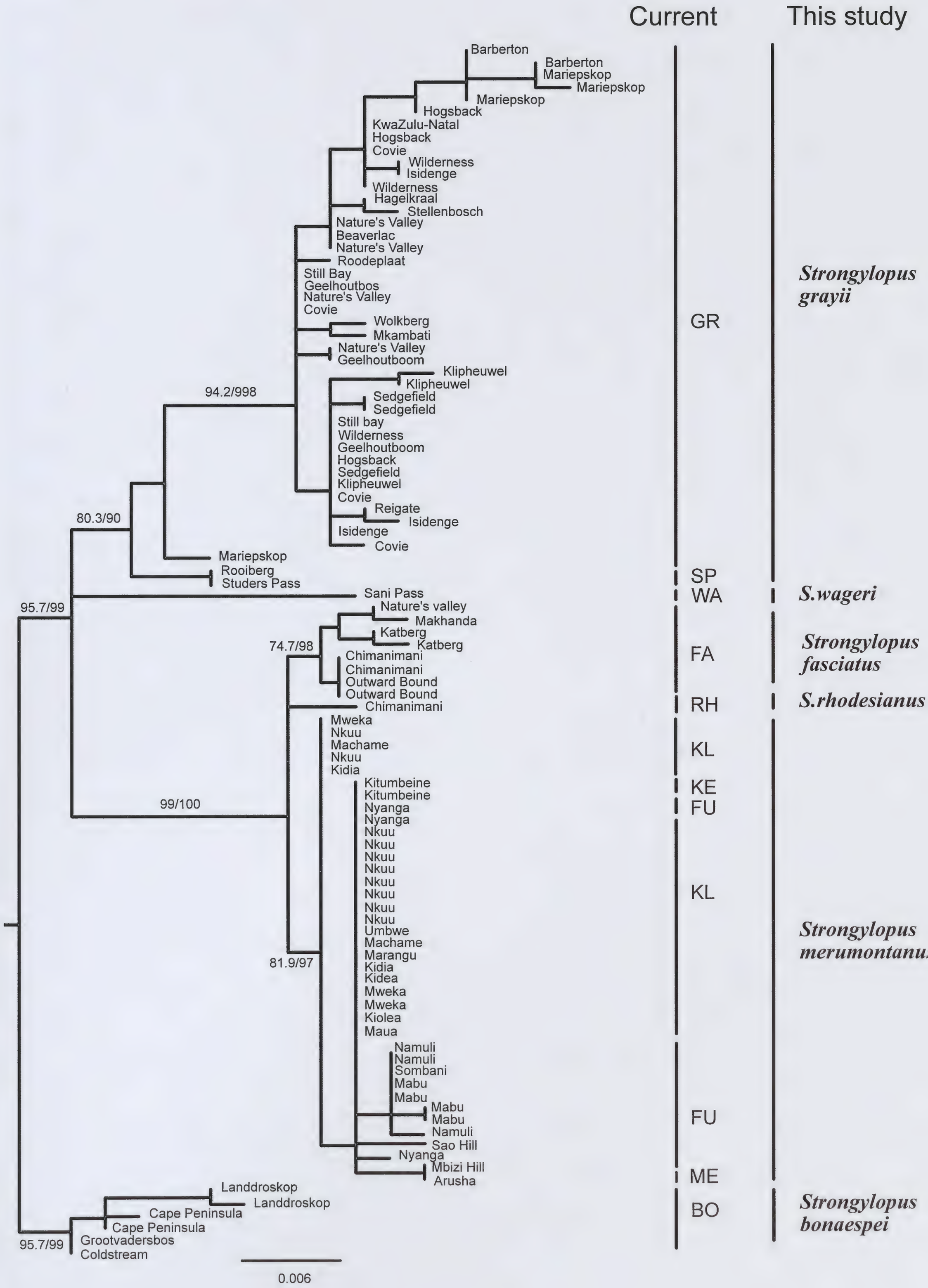

Fig. 3. Phylogeny of the genus *Strongylopus*, based on tyrosinase exon 1. Current name codes: See Figs 1 and 2.

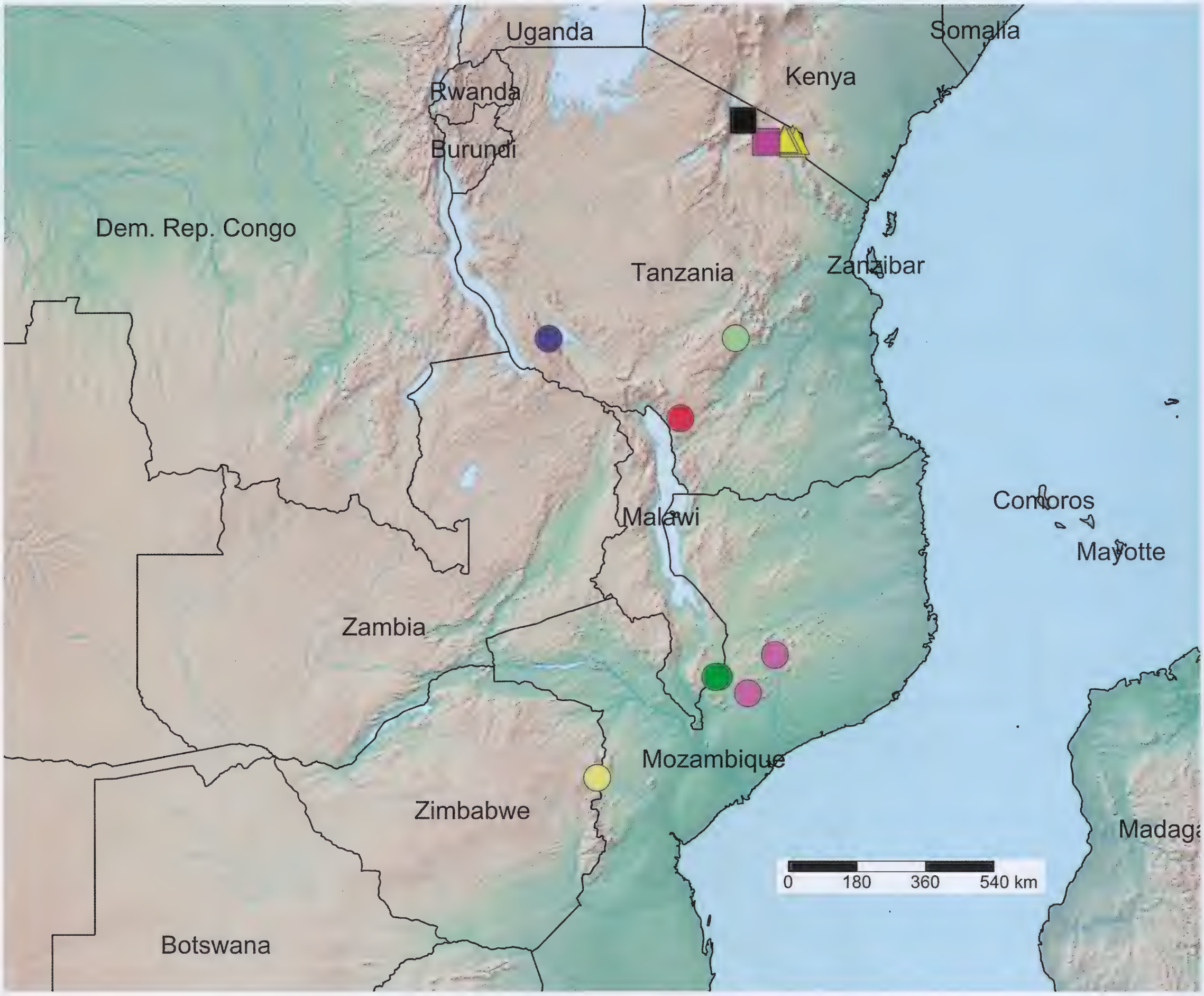

Fig. 4. Location of the sampled populations now recognised as *S. merumontanus*. *Strongylopus merumontanus* – purple square, *S. kitumbeine* – black square, *S. kilimanjaro* – yellow triangles, *S. fuelleborni* Mbizi Hill – blue circle, *S. fuelleborni* Udzungwa Mts. – light green circle, *S. fuelleborni* Livingstone Mts. – red circle, *S. fuelleborni* Mt. Mulanje – green circles, *S. fuelleborni* Mts. Mabu and Namuli–purple circles, *S. fuelleborni* Nyanga – yellow circle.

differences revealed between isolated populations of *S. merumontanus*. Table 4 lists the uncorrected *p* distances between *S. kitumbeine, S. kilimanjaro, S. merumontanus,* and populations of *S. fuelleborni* on Mt. Mulanje, Mts. Namuli and Mabu, Nyanga, Mbizi Hill, and the Udzungwa Mountains. The distances between *S. merumontanus* and the populations of *S. fuelleborni* on Mt. Mulanje and Mts. Namuli and Mabu vary from 1.5 to 2.1%. The distances between *S. merumontanus*, *S. kitumbeine*, *S. kilimanjaro*, and populations of *S. fuelleborni* from Nyanga, Mbizi Hill, the Livingstone Mts. and the Udzungwa Mts. are very similar, varying 0-0.8%. The intraspecific distances for *tyr* and *RAG-1* varied from 0-1.0%, and 0-1.4%, respectively.

Haplotype networks: Haplotype networks using the TCS algorithm are shown in Fig. 5. The mitochondrial 12S rRNA and 16S rRNA, as well as the two nuclear genes showed similar patterns. There was a single shared *RAG-1* haplotype between *S. rhodesianus* and *S. merumontanus* from Nyanga in Zimbabwe. Due to low genetic differences, *S. merumontanus*, *S. fuelleborni*, *S. kitumbeine*, and *S. kilimanjaro* were combined and treated as a single species. The minimum base changes between closely related species are listed in Table 2.

Discordance: Some recent studies have shown discordance between the phylogenies derived from mitochondrial and nuclear genes (Toews & Brelsford, 2012), which is often related to incomplete lineage sorting (Streicher & Day, 2020). The faster rate of divergence of mitochondrial genes compared to nuclear genes in amphibians (Crawford, 2003), should not change the relationships recovered where there is no discordance. Hybridization has been proposed to account for discordance in *Polygonia* butterflies (Wahlberg *et*

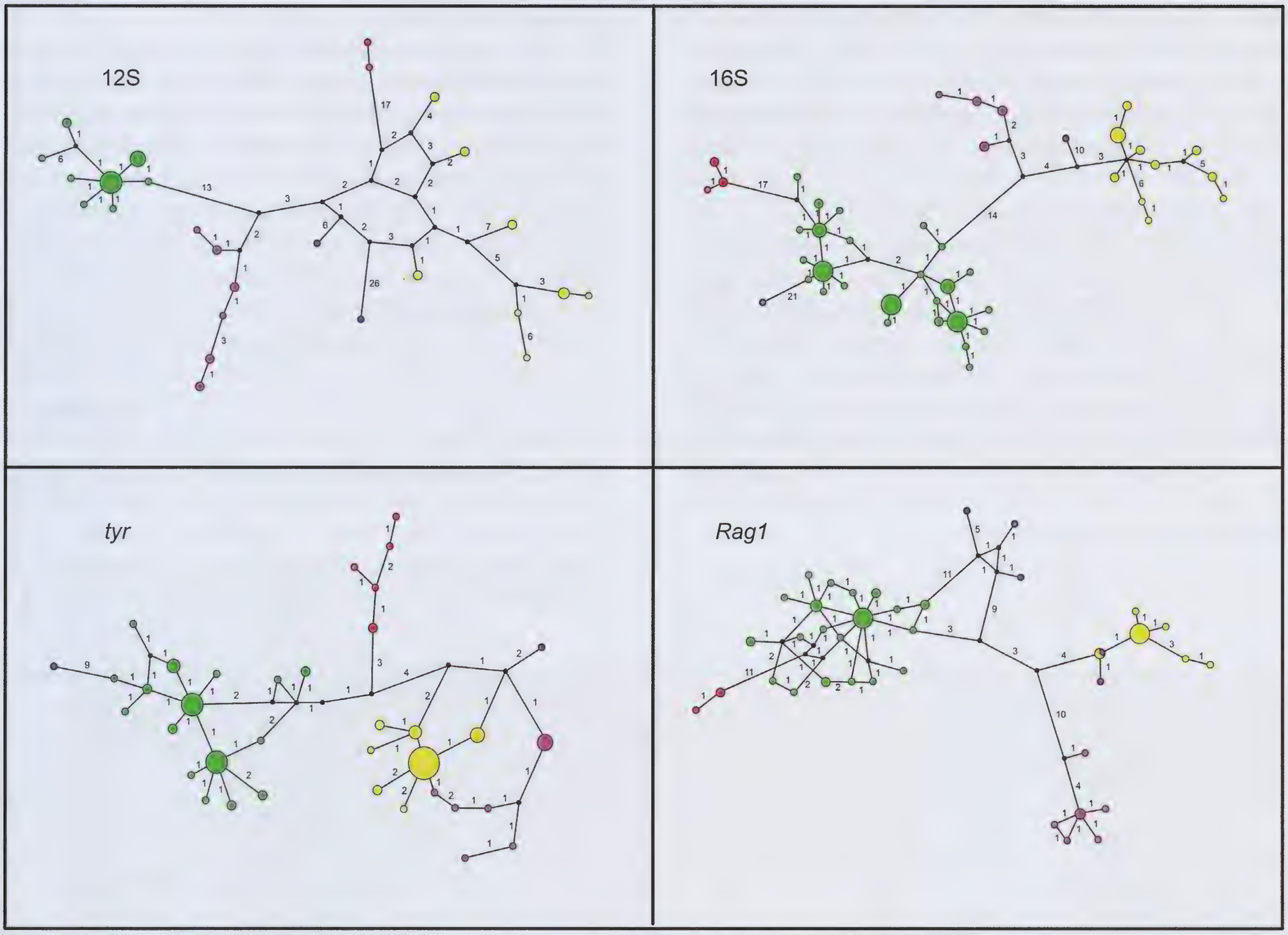

Fig. 5. Haplotype networks for 12S, 16S, tyrosinase exon 1, and *RAG-1*. Size of symbol is relative to number of individuals. Numbers indicate base changes along branch. Black symbols are hypothesised intermediate haplotypes. Green – *S. grayii*, red – *S. bonaespei*, blue – *S. wageri*, violet – *S. fasciatus*, yellow – *S. merumontanus*, purple – *S. rhodesianus*.

Table 2. Minimum base differences between species of *Strongylopus*. See Table 1 for species codes. Data presented as 12S rRNA/16S rRNA/*tyr*/*RAG-1*.

	GRA	FAS	RHO	WAG	MER
GRA					
FAS	19/20/-/-				
RHO		18/22/5/18			
WAG	-/22/10/16		36/-/-/-		
MER		-/-/1/18	-/17/5/0	31/-/-/-	
BON	-/20/10/16				26/-/12/-

al., 2009) and for many cases in amphibians (Toews & Brelsford, 2012). Gonçalves *et al*. (2007) suggested that a deep coalescence was responsible for the discordance in midwife toads *Alytes*, but could not discount the possibility of putative hybridization events causing a reticulated pattern of evolution. Although there may be a difference in the relationships recovered from mitochondrial and nuclear genes, there was no difference in the composition of the clades (species) recovered here. No discordance was found in *Strongylopus*, with the clades (species) strongly supported, similar to the findings of Stöck *et al*. (2008) in the species of *Hyla* found around the Mediterranean, and *Pleuroderma* in South America (Faivovich *et al*., 2012).

Dating (Fig. 6): The split of *Strongylopus* from *Amietia* happened during the early Eocene, 53 Mya (95% HPD [highest posterior density] 83.4-26.8 Mya). The next split during the middle Oligocene was between the ancestor of southern *S. bonaespei* + *S. grayii* + *S. wageri* from the ancestor of northern *S. merumontanus* + *S. fasciatus* + *S. rhodesianus* at 27 Mya (95% HPD 41.3-15.6 Mya). Further splits during the Miocene included the *Strongylopus bonaespei* split from *S. grayii* + *S. wageri* around 22 Mya (95% HPD 34.3-11.7 Mya), followed by the split of *S. grayii* from *S. wageri* around 19 Mya (95% HPD 29.6-8.7 Mya). The *S. rhodesianus* split from the ancestor of *S. fasciatus* + *S. merumontanus* took place at around 16 MYA (95% HPD 22.6-10.8 Mya), followed by the split of *S. fasciatus* from *S. merumontanus* at around 11 Mya (95% HPD 11.7-10.2 Mya). The paleoclimate correlates are discussed below.

Advertisement calls

The calls could be divided into four types. A single amplitude modulated (AM) click, a brief high-pitched frequency modulated (FM) whistle, a chuckle, and a trill (Fig. 7). *Strongylopus grayii* usually produces clicking calls. Brief whistle calls are known for *S. fasciatus* and *S. merumontanus*. A trill is a series of repeated whistles, common in *S. merumontanus*. The chuckle call is part of the *S. bonaespei* vocalisation, often interspersed with croaks. The call of *S. wageri* is best described as a very variable cackle, with an infrequent loud clack or trill. The call of *S. rhodesianus* is unknown. It was previously described as a trill (Channing, 2001) but this was not based on a male whose identification was confirmed by DNA, and may have been a misidentified *S. fasciatus*. Species-specific call characteristics are given with the species summaries below, including the call guilds after Emmrich *et al*. (2020). The call parameters of *S. fuelleborni*, *S. kitumbeine*, and *S. kilimanjaro* are

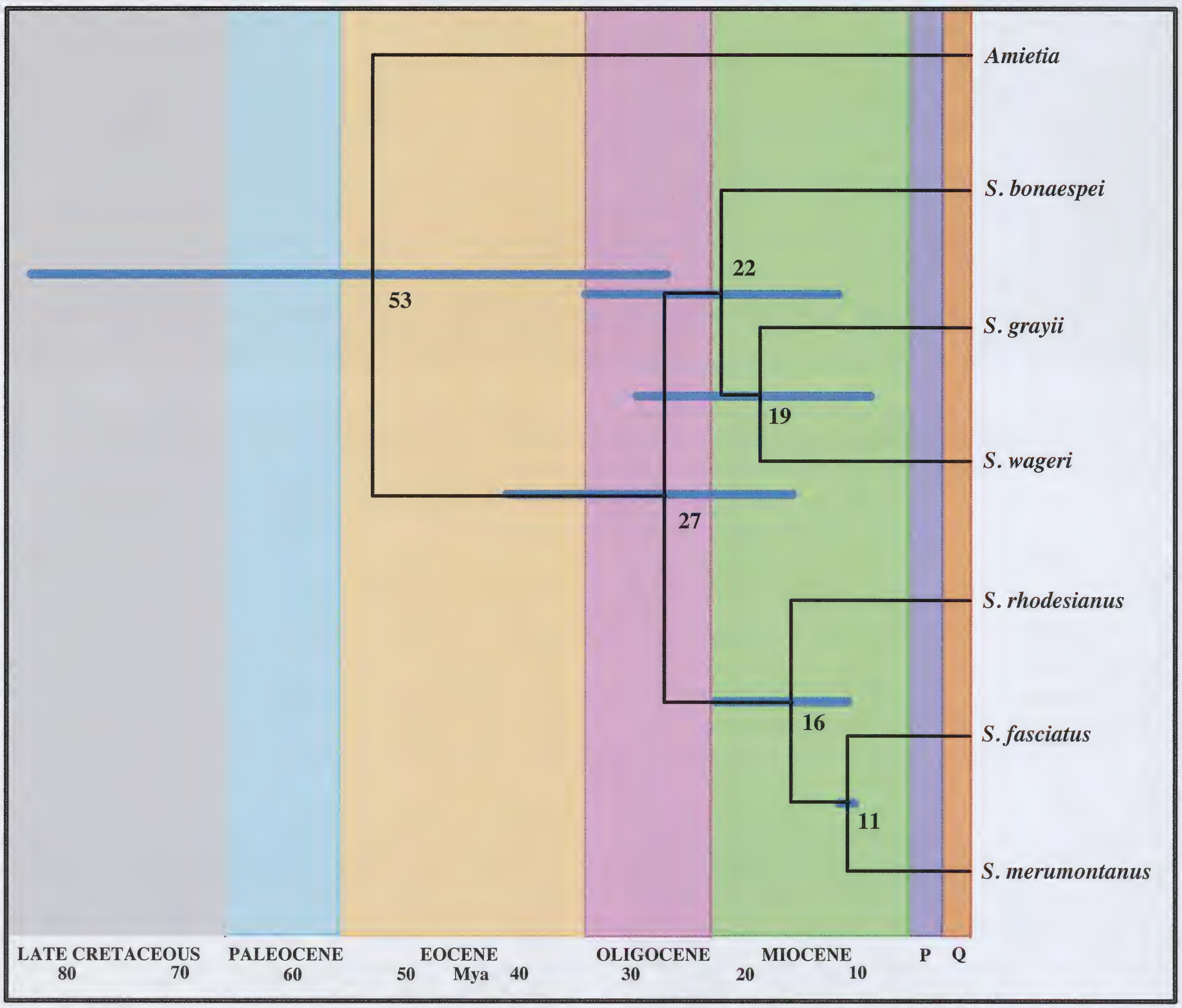

Fig. 6. Divergence estimates based on 16S rRNA. Blue bars indicate 95% HPD. Scale in Ma.

discussed under *H. merumontanus* below, as they are very similar and overlap in structure.

Greig *et al.* (1979) showed differences between the calls of *S. fasciatus* and *S. bonaespei*. Poynton (1964a) remarked that the southern and northern populations of *S. grayii* had slightly different advertisement calls with the northern population having slightly lower pitched calls. Our large sample (474 calls) shows that the range of dominant frequencies, 1464-3030 Hz was not related to latitude (Fig. 8) with a range of frequencies shown in both northern and southern populations.

Morphology

The available frogs of all taxa showed remarkable similarity in most body proportions (Table 3), although there was considerable variation. The largest species in our sample was *S. wageri* with a snout-urostyle length of 50.6 mm. It was closely followed by *S. fuelleborni* (49.3), *S. kilimanjaro* (46.5) and *S. bonaespei* (46.5). Poynton (1964a) gives a maximum size for *S. bonaespei* of 47.5 mm.

The mean snout-urostyle lengths were very similar. *Strongylopus merumontanus* is the shortest (25 mm) while *S. grayii*, *S. springbokensis*, *S. fasciatus*, *S. fuelleborni*, *S. kitumbeine*, *S. kilimanjaro*, *S. wageri*, *S. bonaespei* and *S. rhodesianus* all varied 31.4-40.5 mm.

Strongylopus springbokensis had the shortest legs, as shown by the average value of 0.7 for HW/FOT, although there was considerable overlap shown by all other species of 0.4-0.6.

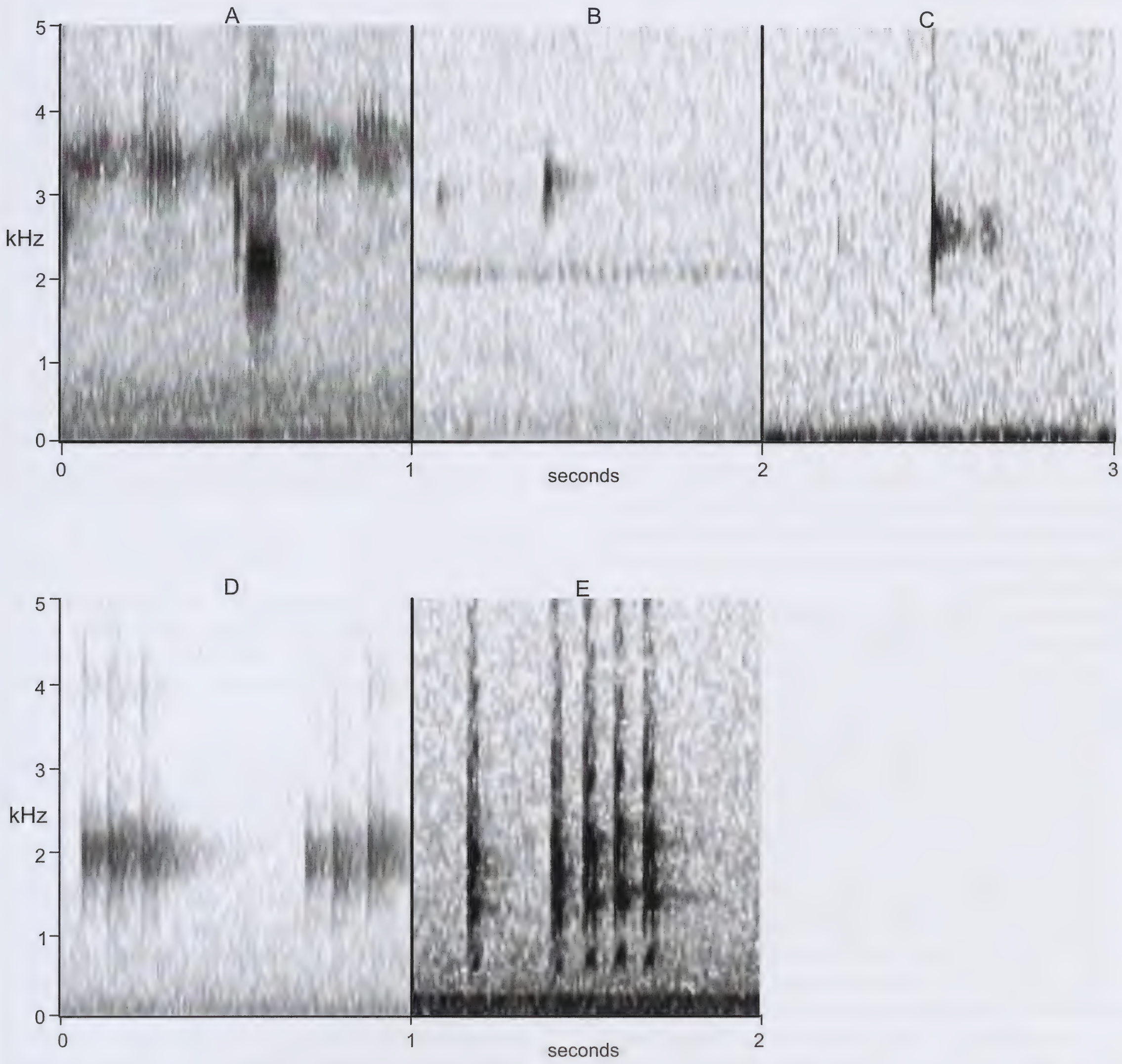

Fig. 7. Representative advertisement calls of the species of *Strongylopus*. A – *S. bonaespei,* B – *S. fasciatus*, C – *S. grayii*, D – *S. merumontanus* (Mt. Kitumbeine), E – *S. wageri*.

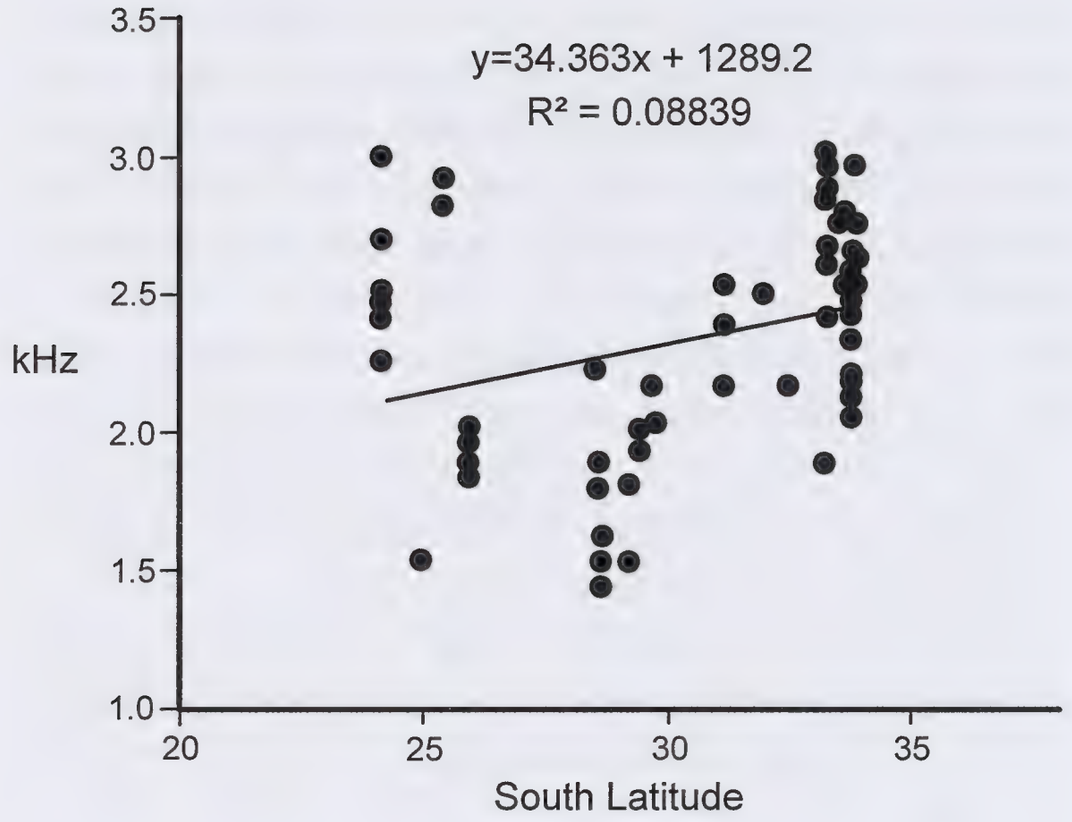

Fig. 8. Dominant frequency of the calls of *S. grayii* vs latitude.

Strongylopus springbokensis also had the shortest hands relative to head width (HW/HND=1.3-2.1) while *S. fasciatus* had the longest hands (HW/HND=0.8-1.2). The other eight species showed intermediate but overlapping values for relative hand length.

Head width as a proportion of body length varied evenly across the species, as shown by the overlap in the proportion SUL/HW (Table 3) for all species.

The largest eyes, as indicated by HW/EW were found in *S. merumontanus* (mean HW/EW=12.0), with the smallest eyes (mean HW/EW=18.3) were found in *S. springbokensis*. However, all species have overlapping ranges in this proportion.

The largest distance between tympanum and eye, as ET/EW, occurred in *S. bonaespei* (mean ET/EW=0.4). All the other species had mean values of 0.3. Body proportions in general were not useful for species identification as there was considerable variation and overlap between all species (Table 3).

The amount of webbing, as indicated by the number of phalanges free of webbing on the fourth (longest) toe, varied from 3-4 within most species, with the most webbing shown by *S. wageri*, where there are 2-3 phalanges free in our sample, often with a margin of webbing to the toe tip. Poynton (1964a) reported 1-3 phalanges free of web in *S. wageri*. Breeding males tend to have more webbing, but this needs to be investigated with a larger sample, or with a long-term field study.

The presence and completeness of dorsal ridges have been used as characters in most species descriptions. Our data revealed that *S. fasciatus* has unbroken vertebral dorsal ridges while *S. grayii*, *S. springbokensis, S. rhodesianus* and *S. bonaespei* have broken ridges, sometimes with a smooth back. *Strongylopus merumontanus, S. fuelleborni, S. kitumbeine* and *S. kilimajaro* have dorsal ridges which are usually continuous, but are often broken or absent. *Strongylopus wageri* has no dorsal ridges.

Colour patterns: Colour patterns have previously been used as diagnostic taxonomic characters by all authors (Figs 9-35). Variable pattern elements in most species include a thin vertebral stripe which may be present or absent, a wide vertebral band, the development of the 'mask' a dark stripe from the nostril through the eye to the arm insertion, a pale triangle on the snout, longitudinal dark stripes running parallel to the dorsal midline, the presence and arrangement of lateral stripes, sometimes broken into rows of spots, the presence and arrangement of dorsal spots or blotches, and the presence of a pale mark running from the anterior corner of the eye to the lower jaw. Overall colour varies from golden brown through dark brown, grey, yellow, orange to red. Stripes and spots are often contrasting in colour. Longitudinal dark stripes along the dorsal midline and laterally are common in *S. fasciatus* and *S. merumontanus*. The variation shown by the different species is detailed below.

Taxonomy

The northern species (*S. merumontanus, S. fuelleborni, S. kitumbeine,* and *S. kilimanjaro*) are similar in genetics, morphology, and advertisement call. They are recognised here as a single species, with *S. merumontanus* being the senior synonym. *Strongylopus springbokensis* is recognised as a junior synonym of *S. grayii*.

Strongylopus bonaespei (Dubois, 1981)

Figs 9-10

Rana (*Strongylopus*) *bonaespei* Dubois, 1981: 929. *Nomen novum* for *Rana fasciata montana* FitzSimons, 1946.

Rana fasciata montana FitzSimons, 1946: 351 (type TMP 20223).

Rana montana. – Greig, Boycott & De Villiers, 1979: 2, figs 7, 10-12 .

Strongylopus montanus. – Channing, 1979: 797, fig. 25.

Strongylopus bonaespei. – Channing, 2001: p. 352, fig. 22.6.

Molecular: The mitochondrial 16S rRNA, nuclear *tyr* and *RAG-1* sequences are remarkably uniform across the range of the species, from the Cape Peninsula in the west to Grootvadersbosch in the east (Table 1, Figs 1, 3).

Morphology: Maximum SUL is 35 mm for males and 48 mm for females (Poynton, 1964a). Snout-urostyle length 3.2 times head width (3.0-3.2). Snout length 1.9 times eye width (1.8-2.1). Eye-nostril distance 1.5 times tympanum width (1.3-1.6). Length of foot 0.8 of SUL (0.7-0.8). Head width 0.41 of foot length (0.40-0.44). Four phalanges of fourth toe free of web. The overall colour is golden brown, although very dark morphs are known. Snout mottled or a pale triangle. A thin dark line runs from the snout through the eye, over the tympanum to the arm. The dark pair of dorsal stripes usually has paired breaks (Poynton, 1964a); cross-banding present on the tibia. There are broken rows of dark paravertebral stripes, or silver and dark stripes (Figs 9, 10). A

Table 3. *Strongylopus* body proportions. Mean and range shown. GRA – *Strongylopus grayii*, SPR – *S. springbokensis*, FAS – *S. fasciatus*, FUE – *S. fuelleborni*, KIT – *S. kitumbeine*, KIL – *S. kilimanjaro*, MER – *S. merumontanus*, WAG – *S. wageri*, BON – *S. bonaespei*, RHO – *S. rhodesianus*. See text for morphological abbreviations.

	GRA (n=29)	SPR (n=7)	FAS (n=21)	FUE (n=15)	KIT (n=2)	KIL (n=5)	MER (n=4)	WAG (n=11)	BON (n=4)	RHO (n=4)
SUL	34.2 (20.8-45.5)	38.0 (33.8-43.3)	36.2 (28.3-41.8)	38.2 (27.4-49.3)	31.4 (23.7-39.2	36.2 (24.4-46.5)	25.0 (20.5-35.2)	37.3 (24.6-50.6)	40.5 (31.7-46.5)	36.1 (30.2-42.3)
HW/FOT	0.5 (0.4-0.6)	0.7 (0.7-0.7)	0.4 (0.3-0.4)	0.4 (0.4-0.5)	0.6 (0.5-0.6)	0.4 (0.4-0.4)	0.5 (0.4-0.6)	0.5 (0.4-0.6)	0.4 (0.4-0.4)	0.43 (0.41-0.6)
SUL/HW	3.0 (2.6-3.3)	2.7 (2.5-2.8)	3.7 (3.1-4.4)	3.2 (2.7-3.7)	2.4 (2.0-2.7)	3.6 (3.4-4.0)	2.8 (2.6-3.0)	2.9 (2.4-3.5)	3.15 (3.0-3.3)	3.2 (3.0-3.5)
SUL/SL	40.4 (24.9-53.1)	45.6 (40.6-51.8)	42.6 (33.7-49.6)	45.4 (32.6-58.0)	38.4 (30.6-46.2)	42.4 (29.2-54.0)	30.1 (24.7-42.1)	44.6 (29.5-60.1)	48.4 (38.2-55.0)	42.8 (36.0-50.2)
HW/EW	14.8 (9.4-20.2)	18.3 (16.6-21.8)	13.5 (11.2-17.3)	15.7 (10.6-19.3)	17.2 (15.8-18.6)	13.7 (9.6-18.2)	12.0 (10.2-15.8)	17.7 (11.6-24.3)	17.0 (13.3-19.3)	15.4 (13.3-17.9)
ET/EW	0.3 (0.2-0.5)	0.3 (0.2-0.4)	0.34 (0.22-0.5)	0.3 (0.2-0.4)	0.3 (0.3-0.4)	0.3 (0.3-0.4)	0.3 (0.2-0.3)	0.3 (0.2-0.4)	0.4 (0.4-0.5)	0.3 (0.3-0.4)
TYM/ET	2.0 (1.3-2.8)	2.4 (1.8-3.0)	1.8 (1.1-2.8)	1.9 (1.5-2.8)	1.7 (1.3-2.2)	1.6 (1.4-2.0)	1.6 (1.1-2.0)	1.67 (1.07-2.4)	1.2 (1.1-1.2)	1.3 (1.2-1.6)
SUL/TIB	1.7 (1.5-2.2)	1.8 (1.7-1.9)	1.5 (1.4-1.8)	1.5 (1.4-1.8)	1.5 (1.2-1.8)	1.6 (1.5-1.7)	1.5 (1.5-1.6)	1.4 (1.3-1.5)	1.5 (1.5-1.5)	1.5 (1.4-1.6)
TIB/FOT	1.0 (0.8-1.0)	1.0 (1.0-1.1)	0.9 (0.7-1.0)	0.9 (0.7-1.0)	0.9 (0.9-0.9)	0.9 (0.9-1.0)	1.0 (0.9-1.0)	1.0 (1.0-1.0)	0.9 (0.9-0.9)	0.9 (0.9-0.9)
HW/HND	1.3 (1.1-1.6)	1.5 (1.3-2.1)	1.0 (0.8-1.2)	1.1 (0.9-1.3)	1.3 (1.3-1.3)	1.0 (0.9-1.1)	1.1 (1.0-1.2)	1.2 (0.9-1.4)	1.2 (1.1-1.3)	1.1 (1.0-1.1)
SL/EW	1.8 (1.5-2.3)	1.9 (1.7-2.9)	1.9 (1.4-2.3)	1.9 (1.5-2.2)	1.7 (1.6-1.8)	1.7 (1.6-2.1)	1.6 (1.5-1.7)	1.6 (1.4-1.9)	1.9 (1.8-2.1)	1.6 (1.5-1.7)
FOT/SUL	0.6 (0.6-0.7)	0.5 (0.5-0.6)	0.8 (0.7-0.8)	0.7 (0.7-0.8)	0.8 (0.6-1.0)	0.7 (0.7-0.7)	0.7 (0.6-0.8)	0.77 (0.6-0.8)	0.8 (0.8-0.8)	0.7 (0.7-0.8)
EN/TYM	1.2 (0.8-1.8)	1.2 (0.8-1.6)	1.3 (1.0-1.9)	1.2 (1.0-1.4)	1.2 (1.1-1.3)	1.4 (1.3-1.8)	1.6 (1.3-2.0)	1.5 (1.1-1.9)	1.5 (1.3-1.6)	1.5 (1.3-2.0)

Figs 9-26. Variation in colour patterns. (9-10) *S. bonaespei*, 9 – Landdroskop, 10 – Cape Peninsula. (11-14) *S. fasciatus,* 11 – George, 12 – Nquado, 13 – Chimanimani, 14 – Sandile's Rest. (15-26) *S. grayii*, 15 – Stellenbosch, 16 – Stellenbosch, 17 – Baviaanskloof, 18 – Little Karoo, 19 – Stellenbosch, 20 – Baviaanskloof, 21 – Cape Town, 22 – Cape Town, 23 –Hogsback, 24 – Langeni, 25 – Cape Point, 26 – Stellenbosch.

vertebral stripe is usually present. There are no brown stripes from behind eyes to urostyle. The ventral surface is immaculate.

Distribution: The distribution falls within the Cape Fold ecoregion of Abell *et al*. (2008). They are known from sea level to the high plateaux of the mountains, in the south-west, extending north along the Cederberg and east to the Tsitsikama Mountains in South Africa (Fig. 36).

Advertisement call: *Strongylopus bonaespei* produces a brief croaking call and a chuckle call (Fig. 7). The duration of the croaking note is 0.083-0.139 s, with 8 or 9 pulses, at a mean pulse rate of 60.8 s^{-1} (50.3-84.3 s^{-1}, n=13). The mean emphasised frequency is 2115 Hz (1987-2231 Hz; n=14). Some calls have the first harmonic suppressed, with the second visible on the sound spectrogram. One individual emphasised both the fundamental frequency and the first harmonic. The chuckle call consists of an initial two notes, followed by three rapidly repeated notes, within 0.8 s (n=1). The call falls into guild E of Emmrich *et al*. (2020).

***Strongylopus fasciatus* (Smith, 1849)**

Figs 11-14

Rana fasciata Smith, 1849: 333, pl. 78, fig. 1; (neotype BMNH 58.11.25.127).
Rana fasciata fasciata. – Barbour & Loveridge, 1928: 197 (by implication).
Strongylopus fasciatus fasciatus. – Van Dijk, 1966: 259.
Rana (*Strongylopus*) *fasciata*. – Dubois, 1981: 250.
Strongylopus fasciatus. – Channing, 2001: 353, fig. 22.7.

Molecular: There are four 16S rRNA haplotypes, of which three overlap geographically, and differ by 1.8% or less. The samples from eastern Zimbabwe are 1.3-2.2% different from the southern population, but are all included in a well-supported clade (Fig. 1). The nuclear *RAG-1* and *tyr* haplotypes show differences of 0-1.1% and show a well-supported clade (Fig. 3).

Morphology: Maximum SUL is 37 mm for males and 50 mm for females (Poynton, 1964a). Snout-urostyle length 3.7 times head width (3.1-4.4). Snout length 1.9 eye width (1.4-2.3). Eye-nostril distance 1.3 times tympanum width (1.0-1.9). Length of foot 0.8 of SUL (0.7-0.8). Head width 0.4 of foot length (0.3-0.4). Fourth toe with 3.5-4 phalanges free of web. Poynton (2013) described this species as possessing characteristic dark-edged skin ridging and stripes. Our samples are overall brown and yellow, with some darker morphs known. There is a pale triangle on the snout. There are two dark continuous paravertebral stripes with a pale vertebral band. A thin dark line runs from the snout through the eye, over the tympanum to the arm. A dark stripe runs from behind the eye to the urostyle, and there are two or three dark lateral stripes. The tibia has mottling or longitudinal stripes. The ventral surface is immaculate.

Distribution: This widespread species is found in six of the ecoregions of Abell *et al.* (2008): Cape Fold, Amatolo-Winterberg Highlands, Southern Temperate Highveld, Zambezian Lowveld, Eastern Zimbabwe Highlands and Zambezian Highveld (Fig. 36). It is known from Zimbabwe, to the South African highveld and east coast.

Advertisement call: *Strongylopus fasciatus* produces a very brief whistle that shows a rise in frequency, or sometimes a high-pitched click (Fig. 7). The mean emphasised frequency is 2854 Hz (1650-3200 Hz, n=361), although a few calls had the fundamental frequency suppressed, with the lowest emphasised frequency being the first harmonic, 5130-6140 Hz (n=30). In three cases, the sound spectrogram showed no harmonics, but only the fundamental frequency. Air temperature does not affect the frequency. The calls fall into guild B of Emmrich *et al*. (2020).

***Strongylopus grayii* (Smith, 1849)**

Figs 15-26

Rana grayii Smith, 1849: 335, plate 78, fig. 2 (lectotype BMNH 58.11.25.138).
Strongylopus grayi. – Steindachner, 1867: 21.
Rana grayi var. *dorsalis* Werner, 1910: 297 (type unknown).
Rana grayi grayi. – Hewitt, 1933.
Dicroglossus grayi. – Deckert, 1938: 138.
Strongylopus grayii. – Van Dijk, 1966: 259
Rana grayii grayii. – Passmore & Carruthers, 1979: 138.
Rana (Strongylopus) grayii. – Dubois, 1981: 250.
Strongylopus springbokensis Channing, 1986: 128, fig. 1 (type PEM A963). **New synonym**
Rana (*Strongylopus*) *springbokensis*. – Dubois, 1992: 259.

Molecular: The 16S rRNA haplotype variation shows a maximum difference of 1.7%. These sequences fall into three groups (Fig. 37): a southwestern clade extending from Namaqualand in the northwest, to the southern Cape (blue square symbols); a southern Cape clade (red triangles); and a northern clade (yellow circles) which extends from northwestern South Africa to the south in the Cape Town area. *Strongylopus springbokensis* is embedded within the southwestern clade. These clades overlap geographically; see the discussion below.
The nuclear *RAG-1* and *tyr* sequences are 0-1.0% different. The *tyr* phylogeny places *S. springbokensis* basal but within a well-supported clade of *S. grayii* sequences (Fig. 3).

Morphology: Values are given for *S. grayii* and *S. springbokensis* separately in Table 3. Body proportions are listed here as *S. grayii*/ *S. springbokensis*. Maximum SUL is 42/42 mm for males and 64/44 mm for females (Channing & Rödel,

2019). Snout-urostyle length is 3.0/2.7 times head width (2.6-3.3/2.5-2.8). Snout length 1.8/1.9 eye width (1.5-2.3/1.7-2.9). Eye-nostril distance 1.2/1.2 times tympanum width (0.8-1.8/0.8-1.8). Length of foot 0.6/0.5 of SUL (0.6-0.7/0.5-0.6). Head width 0.5/0.7 of foot length (0.4-0.6/0.7-0.7). Fourth toe with four phalanges free of web, infrequently three (Poynton, 1964a). These two species are remarkably similar in body proportions, supporting the placement of *S. springbokensis* as a synonym of *S. grayii*.

Our samples (Figs 15-26) are overall brown and grey with yellow, orange or red tinges. There is sometimes a pale triangle on the snout. A thin pale vertebral stripe or wide vertebral band is common. There are no paravertebral stripes, but irregular dark blotches, usually in pairs. A thin dark line runs from the snout through the eye, over the tympanum to the arm. There is usually a thin pale line from the anterior corner of the eye to the upper jaw. A dark stripe runs from behind the eye, through the tympanum to the arm. The tibia has dark cross-banding. An unusual morph with a red dorsum was found in the Langvlei dunes near Wilderness (Jacobsen, 2013). The ventral surface is immaculate, rarely with grey speckles.

Distribution: This widespread species is found in eight of the ecoregions of Abell *et al.* (2008): Karoo, Cape Fold, Amatolo-Winterberg Highlands, Drakensberg-Maluti Highlands, Southern Temperate Highveld, Western Orange (extended to Naukluft). Karoo and Zambesian Lowveld (Figs 36, 37). It is widespread in South Africa, excluding the arid interior. This species was introduced to St Helena Island around 1883 by Miss Phoebe Mary Moss (Barbour, 1934; Mertens, 1971; Ashmole & Ashmole, 2000; Lever, 2003) and they are still present. There are records from Naukluft in central Namibia from 1979 (Channing, 2020), which might represent an introduction. It has not been recently recorded from Naukluft.

Advertisement call: The call of *S. grayii* consists of a sharp, energetic click (Fig. 7). Sometimes the clicks are run together into a trill. The call of *S. springbokensis* from Springbok in Namaqualand is a trill or single click. The dominant frequency of *S. springbokensis* varies from 975 Hz to 1862 Hz (n males=12), while that of *S. grayii* varies from 1464 Hz to 3030 Hz (n males=61). The overlap in call structure and dominant frequency supports placing *S. springbokensis* as a junior synonym of *S. grayii.*

In summary, the duration of the click varies from 0.011-0.028 s. The mean emphasised frequency visible on the sound spectrogram is 2182 Hz (975-3030 Hz, n calls=560), with high energy visible up to 8 kHz. Air temperature does not affect the emphasised frequency. The calls are often produced in chorus, and frequently as a trill. The trills consist of 2-12 notes, at a pulse rate of 12.5-14.9 s^{-1}. Females produce a twittering call during amplexus. The call is classified into guild A (Emmrich *et al.*, 2020).

***Strongylopus merumontanus* (Lönnberg, 1907)**

Figs 27-33

Rana merumontana Lönnberg, 1907: 21, fig. 4 (type NRM 1367).

Rana (*Ptychadena*) *merumontana*. – De Witte, 1921: 7.

Rana fasciata merumontana. – Barbour & Loveridge, 1928: 197.

Strongylopus merumontanus. – Channing & Davenport, 2002: 140.

Rana fülleborni Nieden, 1911: 436 (type ZMB 21773). **New synonym**

Rana (*Ptychadena*) *fuelleborni*. – De Witte, 1921: 7.

Rana fasciata fülleborni. – Loveridge, 1953: 373. – Poynton, 1964a: 203.

Strongylopus fuelleborni. – Channing, 2001: 354, fig. 22.8.

Strongylopus kitumbeine Channing & Davenport, 2002: 137, figs 2-5 (type CAS 225064). **New synonym**

Strongylopus kilimanjaro Clarke & Poynton, 2005: 54, figs 1-2 (type BMNH 1936.2.2.2). **New synonym**

Molecular: The 16S rRNA sequences form a well-supported clade, with recognisable sub-structure with differences varying from 0-2.1%. Isolated populations on the highlands of Mt. Mulanje, Mt. Kilimanjaro, the eastern highlands of Zimbabwe, Mt. Kilimanjaro, Mt. Namuli and Mt. Mabu in Mozambique, and Mt. Kitumbeine (Fig. 4) each show slight differences, with the greatest *p*-distances between Mt. Mulanje in Malawi and Mts Namuli and Mabu in Mozambique and the Udzungwa Mountains in Tanzania (Table 4).

The nuclear *RAG-1* and *tyr* sequences differ by 0-1.4%.

Morphology: The body proportions of *S. merumontanus*, *S. fuelleborni*, *S. kitumbeine* and *S. kilimanjaro* are listed separately in Table 3. The combined values are presented as *S. merumontanus* here. Maximum SUL is 40 mm for males and 53 mm for females (Channing & Rödel, 2019). Snout-urostyle length 3.2 times head width (2.0-4.0). Snout length 1.8 eye width (1.5-2.2). Eye-nostril distance 1.3 times tympanum width (1.0-2.0). Length of foot 0.7 of SUL (0.6-1.0). Head width 0.4 of foot length (0.4-0.6). Fourth toe with four phalanges free of web, infrequently slightly less. Our samples (Figs 27-33) are overall brown to reddish orange. There is sometimes a pale triangle on the snout. A thin pale vertebral stripe or wide vertebral band is common. There is a pair of paravertebral stripes in many populations. A thin dark line runs from the snout through the eye, over the tympanum to the arm. The tibia has cross-banding or a thin longitudinal line. Material from the northern volcanic mountains lacks the ridged paravertebral stripes of the southern *S. fasciatus* (Poynton, 2013). The ventral surface is immaculate or with grey speckles.

Distribution: This widespread species is found in six of the ecoregions of Abell *et al*. (2008): Eastern Zimbabwe Highlands, Mulanje, Coastal East Africa, Lake Malawi, Lake Rukwa, Pangani. It is known from the eastern

Table 4. Uncorrected 16S rRNA *p* distances between populations included in *Strongylopus merumontanus*. Species codes: MER – *S. merumontanus*, FUE – *S. fuelleborni*, KIT – *S. kitumbeine*, KIL – *S. kilimanjaro*.

	MER Mt Meru	FUE Mt. Mulanje	FUE Mts. Namuli & Mabu	FUE Nyanga	FUE Mbizi Hill	FUE Livingstone Mts.	FUE Udzungwa Mts.	KIT Mt Kitumbeine	KIL Mt Kilimanjaro
S. merumontanus	-								
S. fuelleborni Mt. Mulanje	1.5-1.7	0.2							
S. fuelleborni Mts. Namuli & Mabu	1.7-1.9	1.7-2.1	0-0.2						
S. fuelleborni Nyanga	0.8	1.9-2.1	1.3-1.5	0					
S. fuelleborni Mbizi Hill	0	1.5-1.7	1.7-1.9	0.8	-				
S. fuelleborni Livingstone Mts.	0.4	1.5-1.7	1.3-1.5	0.4	0.4	-			
S. fuelleborni Udzungwa Mts.	0.6	1.7-1.9	1.5	0.6	0.6	0.2	-		
S. kitumbeine	0.4	1.5-1.7	1.7-1.9	0.8	0.4	0.4	0.6	0	
S. kilimanjaro	0.4-0.6	1.5-1.9	1.5-1.9	0.8-1.1	0.4-0.6	0.4-0.6	0.6-0.8	0.4-0.6	0-0.2

Figs 27-35. Variation in colour patterns. (27-33) *S. merumontanus*, 27 – *S. fuelleborni* Mt Namuli, 28 – *S. fuelleborni* Mt Mabu, 29 – *S. fuelleborni* Mt Mulanje, 30 – *S. fuelleborni* Kitetele, 31 – *S. kilimanjaro* Mt Kilimanjaro, 32 – *S. kitumbeine* Mt Kitumbeine, 33 – *S. fuelleborni* Mbeya. (34) *S. rhodesianus* – Chimanimani. (35) *S. wageri* – Sani Pass.

highlands of Zimbabwe, the isolated highlands and old volcanic mountains of Malawi, northern Mozambique inselbergs, southern Tanzania, and the Eastern Arc Mountains. It has not been found in the drier lowlands between the Eastern Arc highlands (Fig. 36).

Advertisement call: The advertisement call of *S. fuelleborni* consists of a brief whistle or series of whistles combined into a trill. Each note is frequency modulated, with a rise in pitch, and may contain 1-10 pulses. The dominant frequency varies from 2061 Hz to 3145 Hz (n males=31). The advertisement call of *S. kilimanjaro* consists of a brief whistle or series of whistles combined into a trill. Each note is frequency modulated, with a rise in pitch. The dominant frequency varies from 2667 Hz to 2940 Hz (n males=6). The advertisement call of *S. kitumbeine* consists of a trill with two to eight notes. The dominant frequency varies from 2135 Hz to 2325 Hz (n males=15). The only recorded call of *S. merumontanus* consists of a brief whistle with a dominant frequency of 2663 Hz. The advertisement calls of these northern species overlap in structure and dominant frequency, supporting placing them into a single species.

In summary, the call of *S. merumontanus* consists of a brief whistle or pulsed note, that may be repeated as a trill (Fig. 7). The mean emphasised frequency is 2493 Hz (2061-3145 Hz, n calls=298). The trill consists of two to eight notes at a mean pulse rate of 9.4 s^{-1} (7-11.6 s^{-1}). Whistles are frequency modulated, rising in frequency. Both trills and whistles are heard in the same chorus. The function of the different calls is not known. These calls fall into guilds B and F of Emmrich *et al*. (2020).

Strongylopus rhodesianus (Hewitt, 1933)

Fig. 34

Rana grayi rhodesiana Hewitt, 1933: 12, plate 1 (Type not traced).

Strongylopus grayii rhodesianus. – Van Dijk, 1966: 259.

Strongylopus rhodesianus. – Channing, 2001: 359, fig. 23.3.

Molecular: Only a single specimen was available for sequencing. The two *RAG-1* haplotypes were 0.2% different.

Morphology: Maximum length 40 mm for males and 50 mm for females (Channing & Rödel, 2019). Snout-urostyle length 3.2 times head width (3.0-3.5). Snout length 1.6 eye width (1.5-1.7). Eye-nostril distance 1.5

times tympanum width (1.3-2.0). Length of foot 0.7 of SUL (0.7-0.8). Head width 0.4 of foot length (0.4-0.6). Fourth toe with 3.7-4 phalanges free of web. Our samples (Fig. 34) are overall brown and grey. There is usually a pale triangle on the snout, often continuous with a broad vertebral band. A thin vertebral stripe is absent. The back is usually plain, or with darker irregular blotches. There is a thin pale line from the anterior corner of the eye to the upper jaw. A thin dark line runs from the snout through the eye, over the tympanum to the arm. The tibia has dark cross-bands. The ventral surface is immaculate or with grey speckles.

Distribution: This species is only known from a single ecoregion of Abell *et al*. (2008), the Eastern Zimbabwe Highlands (Fig. 38).

Advertisement call: In light of the presence of three species in the area (*S. merumontanus, S. fasciatus* and *S. rhodesianus*) and the similarity in the calls, there is no confirmed recording of a call where the male has been positively identified by sequencing.

Strongylopus wageri (Wager, 1961)

Fig. 35

Rana wageri Wager, 1961: 151, figs 151, 154 (type NMP 1145).
Strongylopus wageri. – Van Dijk, 1966: 259.
Rana (*Strongylopus*) *wageri*. – Dubois, 1981: 233.

Molecular: Three 16S rRNA sequences were available from the Sani Pass area, which were identical. The nuclear *RAG-1* phased sequences varied from 0.7-1.5%. Only a single *tyr* sequence was available.

Morphology: Maximum SUL is 42 mm for males and 48 mm for females (Channing & Rödel, 2019). Snout-urostyle length 2.9 times head width (2.4-3.5). Snout length 1.6 eye width (1.4-1.9). Eye-nostril distance 1.5 times tympanum width (1.1-1.9). Length of foot 0.7 of SUL (0.6-0.8). Head width 0.5 of foot length (0.4-0.6). Fourth toe with one to three phalanges free of web. There are no dorsal skin ridges. Our samples (Fig. 35) are overall brown. There is a pale triangle or spotting on the snout. A thin pale vertebral stripe is often present. There are irregular dark blotches or fine spots on a uniform dorsal background. A thin dark line runs from the snout through the eye, over the tympanum to the arm. A dark lateral line runs from the arm to the leg. The tibia has dark cross-banding. The ventral surface is immaculate.

Distribution: This species is found in two of the ecoregions of Abell *et al*. (2008): Drakensberg-Maluti Highlands and Southern Temperate Highveld (Fig. 38). It is known from forested areas and mountain slopes.

Advertisement call: *Strongylopus wageri* produces a series of notes that can best be described as a cackle, as the notes are irregularly spaced (Fig. 7). The individual calls (n calls=36) may sound like a cough in some cases. The note rate for cackles varies from 3.6-13.6 s^{-1}, while the coughs show individual pulses with pulse rates of 36.7-129.0 s^{-1}. The mean emphasised frequency is 1319 Hz (682-1563 Hz). The calls fall into guild E of Emmrich *et al*. (2020).

DISCUSSION

Genetic variation: The 16S gene is widely used as a yardstick when discussing species boundaries with 3% difference a general indication of potential species difference (Vences *et al*., 2005; Vietes *et al*., 2009). In the Pyxicephalidae, the 16S uncorrected p-distances between species within a genus varied as follows: *Amietia* 1.3-10.0% (Channing *et al*., 2016), *Anhydrophryne* 6.3-7.6% (Dawood & Stam, 2016), *Arthroleptella* 1.1-6.6% (Turner & Channing, 2008), *Cacosternum* 1.1-7.3% (Channing *et al*., 2013), *Nothophryne* 3.0-6.5% (Bittencourt-Silva *et al*., 2016), and *Tomopterna* 1.0-9.2% (Wilson & Channing, 2019). The distances found between species of *Strongylopus* (2.8-7.4%) found in our study are thus in line with the other pyxicephalid genera.

Substructure in *Strongylopus grayii*: Tolley *et al*. (2010) suggests that gene flow may be restricted between the northern (summer breeding) and southern (winter breeding) populations of *S. grayii*. They recognise a southern clade, which was divided into Southwest (Group 1) and South (Group 2), and a northern clade divided into East (Group 3), Drakensberg (Group 4) and North (Group 5). They also had two samples from the far north, which were not classified. Our study recognised three clades, equivalent to groups 1 and 2 and the northern clade (groups 3+4+5) of Tolley *et al*. (2010) and supports the recognition of a southern and northern clade, with their far northern samples included in the northern clade. However, our study included more samples than were available to Tolley *et al*. (2010), and shows geographical overlap between the northern and southern clades (Fig. 37), with the 'northern clade' extending to Cape Town at the southern tip of Africa, and a greater *p*-distance between individuals of up to 1.7%.

The northern and southern populations of *S. grayii* showed a mean 0.6% difference between populations in 16S sequences (Tolley *et al*., 2010). Tolley *et al*. (2010) found this difference to be "comparable to the level of divergence found between other amphibian species (Turner *et al*., 2004; Vences *et al*., 2005; Measey *et al*., 2007; Channing & Schmitz 2008; Turner & Channing, 2008; Blackburn, 2009)." However, this is a misreading of the literature. Turner *et al*. (2004) found a mean difference between combined 12S and 16S sequences between *Arthroleptella* species of 3.9%; Vences *et al*. (2005) found a mean difference between sibling species of mantellid frogs of about 7% for 16S; Measey *et al*.

(2007) reported a 16S difference between two species of *Ptychadena* of 5.2-5.6%; Channing & Schmitz (2008) found *Cacosternum kinangopensis* to be 4% different for 16S from *C. plimptoni*; Turner & Channing (2008) found 16S differences between species of *Arthroleptella* of 1.7-6.6%; and Blackburn (2009) reported a mean divergence between *Arthroleptis* species of 12.8%, and between *Cardioglossa* species of 8.8%, using the 12S to 16S fragment. The 0.6% difference in 16S sequences found between some northern and southern populations of *Strongylopus* (Tolley *et al*., 2010) or the 1.7% difference in our larger sample is the kind of variation that is expected in a widespread species and reflects intraspecific variation.

Substructure in *Strongylopus merumontanus*: Many of the populations are found on isolated highlands, for example the extinct volcanoes Mt. Kitumbeine

Fig. 36. Distribution of samples. Specimens examined for morphology, advertisement calls, and/or molecular sequences. *Strongylopus merumontanus* – red, *S. fasciatus* – orange, *S. bonaespei* – blue.

(*S. kitumbeine*) Mt. Kilimanjaro (*S. kilimanjaro*) and Mt. Meru (*S. merumontanus*), while *S. fuelleborni* is widely distributed in northeastern Zambia, Malawi and Tanzania (Fig. 4). Although these four populations have previously been recognised as different species, this study has demonstrated a similarity in genetics, advertisement call and morphology. The 16S rRNA uncorrected *p* distances between populations are not large enough to maintain specific status for the northern volcanic species. *Strongylopus merumontanus* has uncorrected *p* values of 0-1.9% compared to all other species in this group. *Strongylopus fuelleborni* from Mt. Mulanje has uncorrected *p* values of 1.5-1.9% between all other populations (Table 4), while the other populations of *S. fuelleborni* have uncorrected *p* values of 0.2-1.9%. The nuclear *tyr* sequences between the populations vary 0-1.0%.

The greater uncorrected 16SrRNA *p* distance of the population of *S. fuelleborni* on Mt. Mulanje compared to other populations may be related to the age of the inselberg. While the volcanoes of northern Tanzania are less than 2 million years old, Mt. Mulanje was formed by erosion of softer soil around the granites of the inselberg that were formed 140 Mya. The long period of isolation is reflected in the presence of at least 69 endemic plant species on Mt. Mulanje (Strugnell, 2002).

New relationships: The relationship between *Strongylopus fasciatus* and *S. merumontanus* has been documented since Barbour & Loveridge (1928) recognised *Rana fasciata merumontana.* Our molecular phylogeny confirmed the relationship, placing these taxa as sister species. *Strongylopus bonaespei* was also described as a subspecies of *Rana fasciata* by FitzSimons (1946), but the molecular phylogeny places *S. bonaespei* basal to all the other species. *Strongylopus rhodesianus* was initially believed to be related to *S. grayii* when it was described by Hewitt (1933) as *Rana grayi rhodesiana.* The molecular phylogeny, however, places *S. rhodesianus* and *S. grayii* in different clades.

Origin of the species: Poynton & Broadley (1985) suggested that the genus shows a progression from primitive taxa in the south, with more derived taxa in the north. Poynton later doubted that there was support for this suggestion, stating that the genus does not easily fit the commonly held pattern of radiation from the south (Poynton, 2013). The southern African rainfall gradient from >1000 mm in the east to <20 mm in the west is reflected in the presence of *Strongylopus* only in the east of the continent, with the exception of a possible introduction of *S. grayii* in central Namibia (Channing, 2020).

Fig. 37. Distribution of the clades within *S. grayii*. Blue symbols – southwest, red symbols – southern, yellow symbols –northern.

We estimated the split of the genus *Strongylopus* from *Amietia* to have happened 53 Mya (95% HPD 26.8-83.4 Mya), during the middle Eocene. At this time all major rifting, igneous intrusions and mountain building had ceased (McCarthy & Rubidge, 2005), when the vegetation in Africa was mostly woodland in areas with intermediate rainfall. The Orange River was formed by the Kalahari River that captured the Karoo River. In the late Eocene the climate began to cool, due to the opening of the Drake Passage, which permitted the circulation of cold oceanic water as the Antarctic ice cap reached a maximum 25-35 Mya (McCarthy & Rubidge, 2005). The cold Benguela current developed at this time (Feakins & de Menocal, 2010), leading to increased southern African aridity. *Strongylopus* is represented mostly by highland species, with the exception of the widespread *S. grayii,* which occurs in a range of habitats from coastal lowlands to the southern African inland plateau. This transition from the Eocene-Oligocene ice-free greenhouse world, to an icehouse climate with the first major glaciation of Antarctica occurring around 34 Mya, lasting only 0.5 Ma (Hutchinson *et al*., 2021).

The earliest split separated the ancestor of the southern species from the ancestral widespread species, which may have been limited to the north. The ancestor of *S. bonaespei* + *S. grayii* + *S. wageri* split from the ancestor of *S. merumontanus* + *S. fasciatus* + *S. rhodesianus* at 27 Mya (95% HPD 15.6-41.3 Mya), during the mid-Oligocene. At around 30 Mya grasslands developed in drier areas, possibly isolating the northern and southern clades, although frog fossils are not sufficient or varied enough to understand what effect, if any, the conditions leading to this climate change had on semi-terrestrial amphibians (McCarthy & Rubidge, 2005).

The early Miocene from about 20 Mya was characterised by warmer global climates (Jacobs, 2004), with grasslands expanding, along with deserts and tundra. During the early Miocene the southwest coast and the Cape Peninsula was an open riparian forest and swamp vegetation until the middle Miocene (Sciscio *et al*., 2016). Uplift of the eastern side of southern Africa started around 20 Mya (McCarthy & Rubidge, 2005). Rain forest trees showed a similar split around 17 Mya (95% HPD 10.5-23.4 Mya) (Couvreur *et al*., 2008). The beginning of the Miocene saw the evolution of mammals into niches left vacant by the Eocene extinction event (McCarthy & Rubidge, 2005). This period was also the start of the final evolution events leading to the six species recognised today.

The central high plateau was formed by uplifting around 20 Mya (Partridge, 1997). Rifting started in east Africa during the Miocene. The uplift of the eastern side of southern Africa reduced rainfall to the interior, leading to a rain shadow to the west of the escarpment (McCarthy & Rubidge, 2005), and a rain shadow in East Africa. An arid corridor started to develop between Namibia and northeast Africa (Bobe, 2006). The reduced rainfall led to the expansion of grasslands, which allowed *S. grayii* to occupy seasonal wetlands. These experienced a stronger rainfall over a shorter period (McCarthy & Rubidge, 2005).

The last two splitting events occurred close together. *Strongylopus bonaespei* split from *S. grayii* + *S. wageri* around 22 Mya, followed by the split between *S. grayii* and *S. wageri* around 19 Mya that may have been related to the expansion of grasslands and reduced rainfall that isolated the two species in highland forest, leading to allopatric speciation. The southwest coast and the Cape Peninsula were covered in riparian forest from the early to middle Miocene (Sciscio *et al.,* 2016). The present *S. bonaespei* distribution largely coincides with the reconstructed Miocene distribution of tropical/sub-tropical forest patches (Roberts *et al.,* 2013).

After 16 Mya there was a climax of warmth (Flower & Kennet, 1994), the mid Miocene Climatic Optimum (Feakins & de Menocal, 2010), followed by the Benguela current becoming intensified (Flower & Kennett, 1994), with the further expansion of grasslands, associated with the growth of the Antarctic ice cap and rapid cooling (McCarthy & Rubidge, 2005). This may have isolated the northern *S. merumontanus* from the southern *S. fasciatus*. *Strongylopus rhodesianus* split from the ancestor of *S. fasciatus* + *S. merumontanus* around 16 Mya. The populations presently on the recent volcanic mountains of northern Tanzania are presumably successful due to orographic rainfall (Poynton, 2013), surrounded by more arid lowlands.

There was a mid-Miocene climatic optimum around 15 Mya. Subsequent climate changes include a major cooling event at 14.1-14.8 Mya, leading to the increase of the East Antarctic ice sheet, with increased seasonality, and a mixture of environments (Hill, 1987). Forests were still common in East Africa at 12 Mya (Bobe, 2006). Mid-Miocene warming was followed by cooling, which led to the retreat of tropical ecosystems and increased seasonality. The split between *Strongylopus fasciatus* and *S. merumontanus* occurred around 11 Mya, with *S. fasciatus* distributed in the grasslands south of the moist mountains where *S. merumontanus* was found. They presently overlap on the Eastern Highlands of Zimbabwe, along with *S. rhodesianus*. This may be the result of recent northward expansion of *S. fasciatus* aided by a stable climate (Cohen *et al*., 2007).

Intense volcanic activity started north of Lake Tanganyika at 10 Mya, which continued until 4 Mya. In East Africa an increase in grassland around 5.4-8.4 Mya was implied by a study of Annonaceae rain forest trees (Couvreur *et al.,* 2008; Senut *et al*., 2009). Drier conditions were indicated by the first appearance of C4 grasses in East Africa around 10 Mya (Uno *et al*., 2006). *Strongylopus bonaespei* and *S. wageri* occur in forest (or where forest was recently present), and their ancestor may have been restricted to moist high elevations. An arid corridor running from Namibia to northeast Africa continued to develop during the Miocene, separating the Central

African forest block from the coastal and montane forests of East Africa (Bobe, 2006).

Between 7-8 Mya the Arctic ice cap expanded, shifting climatic belts to the south (Senut *et al.*, 2009). The Sahara became arid although parts of southern Africa remained relatively tropical. In southern Africa a strong seasonal west coast rainfall regime developed (Hoffmann *et al.*, 2015). The C4 grass expansion that occurred around 10 Mya in East Africa only occurred much later in southern Africa (Hopley *et al.,* 2019). This is shown by the presence of predominantly C3 vegetation in the Hoogland cave in South Africa, 5.3-7.3 Mya (Hopley *et al.*, 2019). During the late Miocene there was increased aridity around 6 Mya (Bobe, 2006), with expansion of grasslands, and evidence of local varied habitats.

The southern African coast was uplifted about 600 m during the last 5 Ma (Partridge, 1997), resulting in the development of the Great Escarpment. East Africa 3-5 Mya was warmer and wetter (Danley *et al.*, 2012), while in southern Africa the cold water Benguela upwelling was initiated 3-5 Mya, resulting in aridification of the adjacent west coast (Hoffmann *et al.*, 2015).

A shift from woodland to grassland occurred just before 4 Mya (de Menocal & Bloemendal, 1995). The populations of *S. fasciatus* have subsequently been able to expand to the south and north, overlapping the northern *S. merumontanus* on the Eastern Highlands of Zimbabwe, with 3-5 Mya characterised by warmer and wetter conditions (Danley *et al.*, 2012). In the northern parts of its range, *S. merumontanus* is restricted to moist highlands. Many of these highlands, such as Mt. Kitumbeine, Mt. Meru and Mt. Kilimanjaro, are relatively recent in origin, having formed in the last two million years (Nonnotte *et al.*, 2008).

The warmest phase of the Pliocene occurred between 3-4 Mya, with sea levels about 30 m higher than today,

Fig. 38. Distribution of samples. Specimens examined for morphology, advertisement calls, and/or molecular sequences. *Strongylopus grayii* – yellow, *S. wageri* – red, *S. rhodesianus* – purple.

and with high latitudes experiencing mild climates (Partridge, 1997). A series of ice ages followed, resulting in desertification starting in East Africa (Senut *et al.*, 2009). The present-day arid conditions along the west coast of southern Africa started around 2.8 Mya.

East Africa and the Lake Malawi basin experienced prolonged drought 135-127 ka when the surrounding watershed was a semidesert, followed by the expansion of grasslands between 120-75 ka around Lake Malawi (Cohen *et al.*, 2007). These conditions would have continued the isolation of populations of *S. merumontanus* on the moist highlands of Mt. Mulanje and surrounding granite inselbergs, the Eastern Arc Mountains and the volcanic highlands of Mt. Kilimanjaro and Mt. Kitumbeine. In the last 70 ka conditions have become more humid and stable (Cohen *et al.*, 2007).

Southern Africa has been called a 'cradle of faunal diversity' (Tolley *et al.*, 2008). *Strongylopus* evolution took place during the Miocene, which is similar to the ages of splits found in *Bradypodion* chameleons (Tolley *et al.*, 2008), *Psammobates tentorius* tortoises (Zhao *et al.*, 2020), killifish in the genera *Nothobranchius* (van der Merwe *et al.*, 2021) and *Poropanchax* (Bragança & Costa, 2019), lizards in the genus *Agama* (Matthee & Flemming, 2002), *Platypleura* cicadas (Price *et al.*, 2007) and sengis in the genus *Elephantulus* (Smit *et al.*, 2007).

Distribution: The distribution of our molecular, morphological and advertisement call samples is shown in Figs 36, 38. The presumed species ranges can be found based on museum records in Poynton (1964a, 2013), Poynton & Broadley (1985), Channing (1986), Channing & Davenport (2002), and Clarke & Poynton (2005). The overall distribution of the genus closely follows the ecosystem regions of Abell *et al.* (2008), which are based on freshwater fish ranges (Table 5). For example, *Strongylopus* species occupy many of the habitats where killifish (*Nothobrachius*) occur, such as headwater floodplains, and marshes, seepage areas and slow-flowing seasonal stream channels (van der Merwe *et al.*, 2021). These ecoregions reflect drainage basins and may prove to be useful for examining distributions of amphibians. The present *S. bonaespei* distribution largely coincides with the reconstructed Miocene distribution of tropical/sub-tropical forest patches (Roberts *et al.*, 2013). A broad division of Africa into biogeographical regions based on plants, birds, amphibians, reptiles and mammals (Linder *et al.*, 2012) did not recognise the highlands occupied by *Strongylopus*. Poynton (2013) pointed out that the one degree scale of the Linder *et al.* (2012) study was too coarse to separate the Afrotemperate region of the high mountains of Tanzania where *Strongylopus* occurs.

The distribution of genetically similar populations of *S. merumontanus* across the presently isolated mountain blocks of East Africa, including the West and East Usambaras, the Nguru and Nguu mountains, the Ulugurus, the Rubeho, Malundwe and Udzungwas is similar to populations of reed frogs *Hyperolius* that also occur on moist montane blocks of the Eastern Arc. Lawson (2010) showed that lineages within *Hyperolius puncticulatus*, the *H. spinigularis* complex, and *H. mitchelli* had separate histories with splits dating from 2.1-15.2 Mya, even though they showed similar distributions.

Field identification of *S. fasciatus* and *S. merumontanus* is not easy, and older museum records may be confused. Overlap in body proportions and colour patterns between species indicates that morphology alone is

Table 5. The distribution of *Strongylopus* species in the ecoregions of Abell *et al.* (2008).

Code	Ecoregion	Species present
559	Lake Malawi	*S. merumontanus* (as *S. fuelleborni*)
560	Zambezian Highveld	*S. fasciatus*
561	Lower Zambezi	*S. merumontanus* (as *S. fuelleborni*)
562	Mulanje	*S. merumontanus* (as *S. fuelleborni*)
563	Eastern Zimbabwe Highlands	*S. fasciatus, S. merumontanus* (as *S. fuelleborni*), *S. rhodesianus*
564	Coastal East Africa	*S. merumontanus* (as *S. fuelleborni*)
565	Lake Rukwa	*S. merumontanus* (as *S. fuelleborni*)
568	Pangani	*S. merumontanus* (as *S. merumontanus, S. kitumbeine,* and *S. kilimanjaro*)
572	Western Orange	*S. grayii*
573	Karoo	*S. grayii* (including *S. springbokensis*)
574	Drakensberg-Maloti Highlands	*S. grayii, S. wageri*
575	Southern Temperate Highveld	*S. fasciatus, S. grayii, S. wageri*
576	Zambezian Lowveld	*S. fasciatus, S. grayii*
577	Amatolo-Winterberg Highlands	*S. fasciatus, S. grayii*
578	Cape Fold	*S. bonaespei, S. fasciatus, S. grayii*

not a useful means of identification. The discovery of *S. merumontanus* on the Eastern Highlands of Zimbabwe close to *S. fasciatus* suggests that more detailed genetic studies are required where these two species overlap. As little as a single base difference separates some *tyr* haplotypes of *S. fasciatus* and *S. merumontanus*, suggesting relatively recent gene flow between these species. Further sampling may discover nuclear haplotypes shared between these two species.

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Appendix 1. Gene sequences of *Strongylopus* taxa used in this study, listing species, voucher, locality, co-ordinates, and GenBank accession numbers.

Species	Voucher	Locality	Latitude	Longitude	12S	16S	*RAG-1*	*Tyr*
S. bonaespei	VUB1221	Cape Peninsula, South Africa	-34.2054	18.4061		DQ347345	DQ347288	DQ347196
S. bonaespei	PEM A14996	Landdroskop, South Africa	-34.0491	19.0096	OK649508	OK649433		OK648617
S. bonaespei	AC2965	Grootvadersbosch NR, South Africa	-33.9848	20.8077	OK649513	OK649437	OK648576	OK648622
S. bonaespei	AC3380	Montague Pass, South Africa	-33.9039	22.4628		OK649479		
S. fasciatus	ZFMK 66444	Little Brak, South Africa	-34.0485	22.2198	DQ019594	AF215412	DQ019513	
S. fasciatus	PEM A15007	Saarsveld, South Africa	-33.9577	22.5325		OK649480		
S. fasciatus	PEM A15009	Wilderness railway line, South Africa	-33.9948	22.5921	OK649544	OK649482		
S. fasciatus	PEM A11167	Reigate Farm; Travisscock wetland, South Africa	-32.5701	27.1832	OK649546	OK649485		
S. fasciatus	PEM A12087	Nqadu Forest, South Africa	-31.4125	28.7327	OK649553	OK649494		
S. fasciatus	GNP_2009_T2	Chimanimani, Mozambique	-19.7644	33.0892		OK605285		
S. fasciatus	ZMB 90085	Chimanimani, Mozambique	-19.7644	33.0892		OK605286		
S. fasciatus	PEM A09073	Nature's Valley, South Africa	-33.9688	23.5598	OK649526	OK649449	OK648588	OK648636
S. fasciatus	AC3217	Hogsback, South Africa	-19.7693	32.9816	OK649541	OK649475	OK648606	OK648663
S. fasciatus	PEM A11424	Fort Fordyce Nature Reserve; Katberg Gate, South Africa	-32.6631	26.4788	OK649545	OK649484	OK648610	OK648666
S. fasciatus	PEM A11799	Fort Fordyce Nature Reserve	-32.6631	26.4788	OK649547	OK649486		
S. fasciatus	PEM A10173	Cape Morgan Nature Reserve, South Africa	-32.7022	28.3508	OK649549	OK649488		OK648668
S. fasciatus	SAIAB 193036	Kweza Trail, Chimanimani, Zimbabwe	-19.7826	33.0408	OK649562	OK649503	OK648612	OK648682
S. fasciatus	AC3220	Above Outward Bound, Zimbabwe	-19.7681	33.0236	OK649534	OK649457	OK648605	OK648644, OK648662

Species	Voucher	Locality	Latitude	Longitude	12S	16S	*RAG-1*	*Tyr*
S. fasciatus	KTH06-01	Gondwana Game Reserve, South Africa	-34.0466	21.8827		GU952052		
S. fasciatus	KTH06-02	Mossel Bay, South Africa	-34.0466	21.8827		GU952053		
S. grayii	ATSLBSGO1	Vergaderingskop Private NR, South Africa	-34.3635	21.5746		GU952048		
S. grayii	STGRHLDB	Driekoppe Farm, Helderberg, South Africa	-34.022	18.8851		GU952077		
S. grayii	MH0846	Berg River Neck, South Africa	-33.9983	19.0114		EF136559		
S. grayii	No voucher	Polka Draai, South Africa	-33.9646	18.7519		HQ014420	HQ014428	
S. grayii	KTH571	Marloth Nature Reserve, South Africa	-33.9469	20.4539		EF136544		
S. grayii	AB009	Stellenbosch, South Africa	-33.9346	18.8667		GU952038		
S. grayii	AB010	Stellenbosch, South Africa	-33.9346	18.8667		GU952039		
S. grayii	AB013	Stellenbosch, South Africa	-33.9346	18.8667		GU952040		
S. grayii	GDKSG1	Groot Drakenstein Mountains, South Africa	-33.9196	19.0391		GU952051		
S. grayii	CF050	Kaaimansgatkloof, South Africa	-33.8992	19.2611		EF136558		
S. grayii	MH1196	Formosa Dam, South Africa	-33.8508	23.6733		EF136557		
S. grayii	MH0325	Louterwater Dam, South Africa	-33.85	23.6731		GU952063		
S. grayii	MH1065	Louterwater Dam, South Africa	-33.85	23.6731		GU952071		
S. grayii	MH1147	Louterwater Dam, South Africa	-33.85	23.6731		GU952072		
S. grayii	MH1108	Perdebond, South Africa	-33.825	21.9264		EF136556		
S. grayii	QRFA1063	Koeberg Nature Reserve, South Africa	-33.6845	18.4365		GU952075		
S. grayii	V222	Buffelsklip Pass, Kamanassieberg, South Africa	-33.6525	22.7542		GU952078		
S. grayii	AB001	Betty's Bay, South Africa	-33.6358	18.8661		GU952035		
S. grayii	AB003	Betty's Bay, South Africa	-33.6358	18.8661		GU952036		
S. grayii	AB006	Betty's Bay, South Africa	-33.6358	18.8661		GU952037		
S. grayii	SGBK2B	Noemakloof, headwaters, South Africa	-33.6175	23.8014		EF136561, GU952076		
S. grayii	AMNH A144979	Bainskloof, South Africa	-33.5798	19.1351		DQ283068		

Species	Voucher	Locality	Latitude	Longitude	12S	16S	*RAG-1*	*Tyr*
S. grayii	ATRVLSG1	Riverlands Nature Reserve, South Africa	-33.4917	18.6047		GU952046		
S. grayii	V174	Die Hel, South Africa	-33.3635	21.6283		EF136560		
S. grayii	ATLAJSG1	Lajuma, South Africa	-33.2225	19.0732		GU952045		
S. grayii	ATRZBSG1	Roodezandberg, Tulbagh, South Africa	-33.2225	19.0732		GU952047		
S. grayii	CF072	Donkerkloof, South Africa	-32.8169	19.3453		GU952049		
S. grayii	MH1336	Cata Hut, South Africa	-32.5647	27.1033		EF136539		
S. grayii	CF519	Upper Krom River, South Africa	-32.5025	19.1625		EF136546		
S. grayii	CF108	Sanddrif, South Africa	-32.4906	19.2656		GU952050		
S. grayii	MEEP XS077	Nico Malan Pass top, Winterberg, South Africa	-32.4583	26.8472		GU952079		
S. grayii	KTH293	Pakhuis Pass, South Africa	-32.1642	19.0367		GU952061		
S. grayii	V194	Gifberg, South Africa	-31.8316	18.7462		EF136536		
S. grayii	V146	Van Rhynsdorp, South Africa	-31.6106	18.7334		EF136537		
S. grayii	MH0644	Upper Quthing Drainage, Lesotho	-30.3994	28.2573		EF136542		
S. grayii	MH0648	Upper Quthing Drainage, Lesotho	-30.3994	28.2573		GU952069		
S. grayii	MH0668	Upper Quthing Drainage, Lesotho	-30.3994	28.2573		EF136543		
S. grayii	QQ0119	Drakensberg, ridge top tarn, South Africa	-29.3513	29.5388		EF136550		
S. grayii	MH0320	Kokoatsane Valley, back of the saddle, Lesotho	-28.9204	29.0658		EF136540		
S. grayii	MH0487	Above Cathedral Peak, South Africa	-28.8973	29.0258		GU952066		
S. grayii	MH0642	Drakensberg, South Africa	-28.877	28.9543		EF136549		
S. grayii	MH0638	Liholohake, Lesotho	-28.6897	28.7621		EF136538		
S. grayii	MH0643	Liholohake, Lesotho	-28.6897	28.7621		GU952068		
S. grayii	MH0450	Upper Kgotjoane, Lesotho border, South Africa	-28.6594	28.70391		GU952065		
S. grayii	QQ0126	Mechachaneng Stream, Lesotho	-28.6515	28.7008		EF136547		
S. grayii	MH0608	Drakensberg, South Africa	-28.6486	28.714		EF136552		
S. grayii	MH0449	Phuthaditjaba, South Africa	-28.6223	28.7795		GU952064		
S. grayii	MH0633	Nelson's Kop, South Africa	-28.2336	29.4422		EF136541		

Species	Voucher	Locality	Latitude	Longitude	12S	16S	*RAG-1*	*Tyr*
S. grayii	MH0636	Nelson's Kop, South Africa	-28.2336	29.4422		GU952067		
S. grayii	QQ0359	Normandien Pass, South Africa	-27.9661	29.6855		GU952074		
S. grayii	MH0315	Suikerbosrand, Heidelberg, South Africa	-26.4833	28.25		GU952062		
S. grayii	MH0733	Suikerbosrand, Heidelberg, South Africa	-26.4833	28.25		GU952070		
S. grayii	MPU027	Mt Sheba Road, South Africa	-24.9094	30.6939		EF136554		
S. grayii	MPU030	Mt Sheba Road, South Africa	-24.9094	30.6939		GU952073		
S. grayii	SGMK1	Quarry near Waterberg summit, South Africa	-24.4547	27.6147		EF136553		
S. grayii	MA10	Stellenbosch, South Africa	-33.9346	18.8667	DQ022342			
S. grayii	MHNG 2690.028	Klipheuwel, South Africa	-33.7009	18.6988	OK649509	KC756281	OK648572	OK648618
S. grayii	TM 84854	Barberton, South Africa	-25.7884	31.0532	OK649512	DQ022367		OK648621
S. grayii	AC2966	Stillbay, South Africa	-34.3693	21.4074	OK649514	OK649438	OK648577	OK648623
S. grayii	AC3083	Groot Hagelkraal, South Africa	-34.7	19.5666	OK649516	OK649439	OK648578	OK648625
S. grayii	AC3137	Klipheuwel, South Africa	-33.7009	18.6988	OK649518	OK649441	OK648581	OK648628
S. grayii	PEM A14999	Stellenbosch, South Africa	-33.9346	18.8667		OK649481	OK648580	OK648627
S. grayii	PEM A15003	Hogsback, South Africa	-32.5951	26.9322	OK649524	OK649447	OK648586	OK648634
S. grayii	PEM A15004	Klipheuwel, South Africa	-32.5951	26.9322	OK649525	OK649448	OK648587	OK648635
S. grayii	PEM A09074	Nature's Valley, South Africa	-33.9761	23.5611	OK649527	OK649450	OK648589	OK648637
S. grayii	PEM A09071	Covie, South Africa	-33.95	23.6	OK649528	OK649451	OK648590	OK648638
S. grayii	PEM A09072	Covie, South Africa	-33.95	23.6	OK649529	OK649452	OK648591	OK648639
S. grayii	PEM A13446	Nature's Valley, South Africa	-33.9688	23.5598	OK649530	OK649453	OK648592	OK648640
S. grayii	PEM A09387	Geelhoutboom River, South Africa	-33.7983	25.0619	OK649531	OK649454		OK648641
S. grayii	PEM A15001	Wilderness, South Africa	-33.994	22.5748	OK649535	OK649458	OK648595	OK648645
S. grayii	PEM A15002	Wilderness, South Africa	-33.994	22.5748	OK649536	OK649459		OK648646
S. grayii	PEM A15000	Sedgefield, South Africa	-34.0226	22.8075	OK649519	OK649442	OK648609, OK648582	OK648665, OK648629
S. grayii	PEM A11948	Mkambati Nature Reserve, South Africa	-31.2967	29.9758	OK649548	OK649487		OK648667
S. grayii	PEM A10977	Geelhoutbos Baviaanskloof, South Africa	-33.6338	24.2439	OK649550	OK649489		OK648669
S. grayii	PEM A11805	Isidenge State Forest, South Africa	-32.67	27.2783	OK649551	OK649490		OK648670

Species	Voucher	Locality	Latitude	Longitude	12S	16S	*RAG-1*	*Tyr*
S. grayii	PEM A11163	Roodeplaat, Baviaanskloof, South Africa	-33.6036	25.0753	OK649552	OK649491		OK648671
S. grayii	PEM A11164	Reigate Farm, South Africa	-32.5701	27.1832		OK649492		OK648672
S. grayii	PEM A13468	Coldstream, South Africa	-31.9646	23.7152		OK649493		OK648673
S. grayii	SAIAB 96953	Grey Dam, Makhanda, South Africa	33.3205	26.5208	OK649559	OK649500		OK648679
S. grayii	SAIAB 200301	Beaverlac, South Africa	-32.9079	19.0672	OK649560	OK649501	OK648611	OK648680
S. grayii	NMB A8071	Wolkberg, South Africa	-24.0072	30.0764	OK649515, OK649506	OK649478	OK648608	OK648624
S. grayii	KTH06-48	Noordhoek, South Africa	-34.1094	18.3765		GU952054		
S. grayii	KTH06-50	Noordhoek, South Africa	-34.1094	18.3765		GU952055		
S. grayii	KTH06-52	Noordhoek, South Africa	-34.1094	18.3765		GU952056		
S. grayii	KTH06-54	Noordhoek, South Africa	-34.1094	18.3765		EF136551		
S. grayii	KTH07-83	Koeberg Nature Reserve, South Africa	-33.6846	18.4366		GU952057		
S. grayii	KTH07-86	Koeberg Nature Reserve, South Africa	-33.6401	18.4316		GU952058		
S. grayii	AB08-01	Blyde River Nature Reserve, South Africa	-27.9663	29.6855		GU952041		
S. grayii	AB08-01	Mariepskop, South Africa	-27.9663	29.6855	OK649520	OK649443	OK648583	OK648630
S. grayii	AB08-02	Blyde River Nature Reserve, South Africa	-24.5619	30.8931		GU952042		
S. grayii	KTH08-02	Eastern Escarpment, KwaZulu-Natal, South Africa	-27.9663	29.6856	OK649521	GU952059		OK648631
S. grayii	KTH08-03	Mariepskop, South Africa	-27.9663	29.6856		GU952060		
S. grayii	AB08-03	Mariepskop, South Africa	-27.9663	29.6855	OK649522	GU952043	OK648584	OK648632
S. grayii	AB08-04	Mariepskop, South Africa	-24.5396	30.8725		GU952044		
S. grayii	NMB A8073	Rooiberg, South Africa	-30.4044	18.1016	OK649523	OK649446	OK648585	OK648633
S. grayii	PEM A15008	Studers Pass, Namaqualand, South Africa	-30.4281	18.0616	OK649561	OK649502		OK648681
S. merumontanus	RdS 994	Sao Hill, Tanzania	-8.2233	35.1671				KC180300
S. merumontanus	G56	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492			OK648603	OK648659
S. merumontanus	G57	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492			OK648604	OK648660

Species	Voucher	Locality	Latitude	Longitude	12S	16S	*RAG-1*	*Tyr*
S. merumontanus	PEM A11187	Mount Mabu summit, Mozambique	-16.2968	36.3924				OK648675
S. merumontanus	CAS 225064	Mt Kitumbeine, Tanzania	-2.9044	36.235	OK649543	OK649431		OK648615
S. merumontanus	PEM A14994	Mbizi Hill Forest Reserve, Tanzania	-7.8932	31.6808	OK649507	OK649432	OK648571	OK648616
S. merumontanus	UDSM 2323	Maua Rt, Mount Kilimanjaro, Tanzania	-3.1699	37.4359	OK649510	OK649434	OK648573	OK648619
S. merumontanus	PEM A14997	Mount Kitumbeine, Tanzania	-2.9044	36.235		OK649435	OK648574	OK648685
S. merumontanus	CAS 225065	Mount Kitumbeine, Tanzania	-2.9044	36.235	OK649543	OK649511	OK648575	OK648620
S. merumontanus	AM5755	Nkweseko, Mt Kilimanjaro, Tanzania	-3.1824	37.2426		OK649461		
S. merumontanus	AM4758	Mweka Dam, Mt Kilimanjaro, Tanzania	-3.2167	37.3425		OK649464		
S. merumontanus	MTSN 9392	Mdandu FR, Livingstone Mts, Tanzania	-9.776	34.7818		OK649477		
S. merumontanus	PEM A11650	Mount Namuli, Mozambique	-15.3749	37.0168		OK649483		
S. merumontanus	SAIAB 96468	Thuchila hut, Mt Mulanje, Malawi	-15.8957	35.6096	OK649557	OK649498		
S. merumontanus	UDSM 1609	Mt Meru, Tanzania	3.2479	36.8103		OK649430		OK648614
S. merumontanus	RH001	Nyanga, Zimbabwe	-18.3061	32.8335	OK649532	OK649455	OK648593	OK648642
S. merumontanus	RH002	Nyanga, Zimbabwe	-18.22	32.7463	OK649533	OK649456	OK648594	OK648643
S. merumontanus	AM4654	Mweka Dam, Mt Kilimanjaro, Tanzania	-3.2167	37.3425	OK649537	OK649460	OK648596	OK648647
S. merumontanus	AM4756	Marangu Route, Mt Kilimanjaro, Tanzania	-3.2228	37.5146		OK649462	OK648597	OK648648
S. merumontanus	AM4757	Kidia Forest, Mt Kilimanjaro, Tanzania	-3.2803	37.4406		OK649463	OK648598	OK648649
S. merumontanus	G111	Kidia Forest, Mt Kilimanjaro, Tanzania	-3.2803	37.4406	OK649538	OK649465	OK648684	OK648650
S. merumontanus	GTASF	Machame, Mt Kilimanjaro, Tanzania	-3.1753	37.228	OK649539	OK649466	OK648599	OK648651
S. merumontanus	GL	Mweka Dam, Mt Kilimanjaro, Tanzania	-3.2166	37.3425		OK649467		OK648652
S. merumontanus	GL	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492	OK649540	OK649468	OK648600	OK648653
S. merumontanus	G51	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492		OK649469		OK648654

Species	Voucher	Locality	Latitude	Longitude	12S	16S	*RAG-1*	*Tyr*
S. merumontanus	G52	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492		OK649470	OK648601	OK648655
S. merumontanus	G53	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492		OK649471		OK648656
S. merumontanus	G54	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492		OK649472	OK648602	OK648657
S. merumontanus	G55	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492		OK649473		OK648658
S. merumontanus	ZMB 79033	Nkuu, Mt Kilimanjaro, Tanzania	-3.1797	37.2492	OK649505	OK649474		OK648661
S. merumontanus	MTSN 5298	Kiolela, Udzungwa Mts, Kilolo, Tanzania	-7.8835	36.0893	OK649542	OK649476	OK648607	OK648664
S. merumontanus	PEM A11359	Mount Namuli, Mozambique	-15.3877	37.0434	OK649554	OK649495		OK648674
S. merumontanus	PEM A11184	Mount Mabu, Mozambique	-16.2825	36.3816	OK649555	OK649496		OK648676
S. merumontanus	PEM A11352	Mount Namuli, Mozambique	-15.3877	37.0434	OK649556	OK649497		OK648677
S. merumontanus	SAIAB 96468	Between Sombani and Madzeka, Mt Mulanje, Malawi	-15.893	35.698	OK649558	OK649499		OK648678
S. rhodesianus	SAIAB 193037	Kweza Trail, Chimanimani, Zimbabwe	-19.7826	33.0408	OK649563	OK649504	OK648613	OK648683
S. wageri	J2J_Sw	Mkhomazana River, Sani Pass, South Africa	-29.6	29.35		FJ411441	FJ411457	
S. wageri	J3J_Sw	Mkhomazana River, Sani Pass, South Africa	-29.6	29.35		FJ411442	FJ411458	
S. wageri	AC3059	Sani Pass lower border, South Africa	-29.6128	29.3333	OK649517	OK649440	OK648579	OK648626

Appendix 2. Localities of *Strongylopus* advertisement call recordings, listing species, locality, co-ordinates and number of calls.

Species	Locality	Latitude	Longitude	n
S. bonaespei	George, South Africa	-33.9881	22.4529	1
S. bonaespei	Grootvadersbosch NR, South Africa	-33.9848	20.8077	5
S. bonaespei	Kleinmond, South Africa	-34.3353	19.0126	8
S. fasciatus	Fairview Farm, South Africa	-29.3552	30.5280	34
S. fasciatus	Geelhoutboom River, South Africa	-33.7983	25.0619	17
S. fasciatus	Gonubie, South Africa	-32.9422	28.0098	18
S. fasciatus	Himeville, South Africa	-29.7467	29.5136	54
S. fasciatus	Impendle, South Africa	-29.6005	29.8656	13
S. fasciatus	Lark Rise, South Africa	-29.7699	29.4641	122
S. fasciatus	Longmore Forest Station, South Africa	-33.8583	25.2080	14
S. fasciatus	Loteni Nature Reserve, South Africa	-29.5041	29.5462	20
S. fasciatus	Mazeppa Bay, South Africa	-32.4742	28.6416	11

Species	Locality	Latitude	Longitude	n
S. fasciatus	Oslo Beach, South Africa	-30.7585	30.4386	2
S. fasciatus	Pevensey, South Africa	-29.7830	29.5000	15
S. fasciatus	Pietermaritzburg, South Africa	-29.6006	30.3794	6
S. fasciatus	Pumula, South Africa	-30.6434	30.5264	16
S. fasciatus	The Lakes, South Africa	-33.9833	35.4666	13
S. fasciatus	Touws River, South Africa	-33.3398	20.0271	6
S. fasciatus	Rusito Mission, Zimbabwe	-20.0363	32.8621	40
S. grayii	Elandsbay, South Africa	-31.3141	18.3441	48
S. grayii	Fairview Farm, South Africa	-29.3552	30.5280	14
S. grayii	Firgrove, South Africa	-34.0561	18.7883	45
S. grayii	Gamkaskloof, South Africa	-33.3558	21.7081	2
S. grayii	Geelhoutboom River, South Africa	-33.7983	25.0619	28
S. grayii	Hogsback, South Africa	-32.5951	26.9322	10
S. grayii	Jonaskop, South Africa	-33.9716	19.5063	10
S. grayii	Jonkershoek, South Africa	-33.9686	18.9346	22
S. grayii	Klipheuwel, South Africa	-33.7009	18.6988	4
S. grayii	Lemoenputs, Namibia	-24.2666	16.0500	29
S. grayii	Mooiplaas, South Africa	-26.0961	30.8786	24
S. grayii	Pakhuis Pass, South Africa	-32.1363	19.0081	3
S. grayii	Pietermaritzburg, South Africa	-29.6006	30.3794	24
S. grayii	Rondeberg, South Africa	-33.4244	18.3047	74
S. grayii	Solitude, South Africa	-28.9000	30.8666	21
S. grayii	Stellenbosch, South Africa	-33.9346	18.8667	60
S. grayii	The Lakes, South Africa	-33.9833	35.4666	14
S. grayii	Vrolijkheid Nature Reserve, South Africa	-33.9195	19.8782	19
S. grayii	Bovlei Farm, South Africa	-30.2204	18.0475	31
S. grayii	Paradise Kloof, South Africa	-28.3275	17.0066	52
S. grayii	Springbok, South Africa	-29.6823	17.8872	5
S. grayii	Richtersveld National Park, South Africa	-28.3276	17.0063	32
S. merumontanus	Chelinda, Malawi	-10.5907	33.8136	37
S. merumontanus	Iringa, Tanzania	-7.7681	35.6861	19
S. merumontanus	Kitulo National Park, Tanzania	-9.0630	33.8479	15
S. merumontanus	Lilongwe, Malawi	-13.9943	33.7691	1
S. merumontanus	Luwawa, Malawi	-12.1199	33.7213	4
S. merumontanus	Mbizi Hill Forest Reserve, Tanzania	-7.8931	31.6808	3
S. merumontanus	Mount Kilimanjaro, Tanzania	-3.1753	37.2208	36
S. merumontanus	Mount Kitumbeine, Tanzania	-2.9044	36.2350	16
S. merumontanus	Mount Mabu, Mozambique	-16.2825	36.3816	54
S. merumontanus	Mount Meru, Tanzania	3.2479	36.8103	10
S. merumontanus	Nguu Forest Reserve, Tanzania	-3.1798	37.2492	26
S. merumontanus	Udzungwa Mountains, Tanzania	-7.7731	36.7941	23
S. merumontanus	Ukaguru Mountains, Tanzania	-6.4254	36.9670	15
S. merumontanus	Uluguru Mountains, Tanzania	-6.1050	37.6541	30
S. wageri	Entumeni, South Africa	-28.8889	31.4643	10
S. wageri	Lundy's Hill, South Africa	-29.7256	29.9372	26

Appendix 3. *Strongylopus* specimens examined for morphology, listing species, voucher, locality and co-ordinates.

Species	Voucher	Locality	Latitude	Longitude
S. bonaespei	PEM A14996	Landdroskop, South Africa	-34.0491	19.0119
S. bonaespei	PEM A14997	Landdroskop, South Africa	-34.0491	19.0119
S. bonaespei	PEM A15005	Rockview Dam, South Africa	-34.1956	18.9495
S. bonaespei	PEM A15006	Rockview Dam, South Africa	-34.1956	18.9495
S. fasciatus	PEM A15007	Saarsveld, South Africa	-33.9600	22.5300
S. fasciatus	PEM A15009	Wilderness, South Africa.	-33.9967	22.6001
S. fasciatus	PEM A11161	Groendal Nature Reserve, Rooikrans, South Africa	-33.7131	25.2900
S. fasciatus	PEM A11426	Next to dam at Katberg gate, Fort Fordyce Nature Reserve, South Africa	-32.6631	26.4789
S. fasciatus	PEM A11800	Fort Fordyce NR, vlei north of office, South Africa	-32.6786	26.4883
S. fasciatus	PEM A11803	Sandiles Rest, bottom trout dam, South Africa	-32.6639	27.2992
S. fasciatus	PEM A11804	Sandiles Rest, bottom trout dam, South Africa	-32.6639	27.2992
S. fasciatus	PEM A12357	Mazeppa Bay, pond midway to Manubi Forest, South Africa	-32.5297	28.6304
S. fasciatus	PEM A12359	Mazeppa Bay, pond midway to Manubi Forest, South Africa	-32.5297	28.6304
S. fasciatus	PEM A12416	The Island Nature Reserve, Trap 1, South Africa	-33.9875	25.3426
S. fasciatus	PEM A12422	The Island Nature Reserve, Trap 5, South Africa	-33.9792	25.3721
S. fasciatus	PEM A13872	Ingeli Lodge Outdoor Wedding Venue, South Africa	-30.5426	29.6801
S. fasciatus	PEM A8651	Driefontein, Mvuma, Zimbabwe	-19.4169	30.7144
S. fasciatus	PEM A8739	Natural Pool above (to east) Prime Minister's Lodge, Sehla-ba-Thebe, Lesotho	-29.8578	29.1236
S. fasciatus	PEM A9070	Covie, near Natures Valley, South Africa	-33.9500	23.6017
S. fasciatus	PEM A9073	Nature's valley, South Africa	-33.9761	23.5611
S. fasciatus	MHNG 1295.73	Selbourne, Nyanga, Zimbabwe	-18.3834	32.7044
S. fasciatus	MHNG 2162.80	Giant's Castle National Park, Drakensberg, 2000m, South Africa	-29.0720	29.4287
S. fasciatus	MHNG 2688.66	Drakensberg Gardens, road near Underberg, South Africa	-29.7533	29.4244
S. grayii	MHNG 2690.28	Klipheuwel flooded wheat field, South Africa	-33.6968	18.7243
S. grayii	PEM A14998	Stellenbosch, South Africa	-33.9321	18.8600
S. grayii	PEM A14999	Stellenbosch, South Africa	-33.9321	18.8601
S. grayii	PEM A15000	Sedgefield, South Africa	-26.9322	22.8328
S. grayii	PEM A15003	Hogsback, South Africa	-32.5951	26.9322
S. grayii	PEM A15004	Hogsback, South Africa	-32.5951	26.9322
S. grayii	PEM A11428	Top of Katberg pass, Devil's Bellow, Katberg, South Africa	-32.4272	26.6575
S. grayii	PEM A12229	Darling, pond at entrance to town, South Africa	-33.3775	18.3831
S. grayii	PEM A11678	Bergvliet, South Africa	-34.0572	18.4550
S. grayii	PEM A12418	The Island Nature Reserve, Trap 3, South Africa	-33.9835	25.3407
S. grayii	PEM A12420	The Island Nature Reserve, Trap 5, South Africa	-33.9792	25.3721
S. grayii	PEM A13559	Finella Falls, gate to falls, South Africa	-32.3729	26.3569
S. grayii	PEM A13863	Mpur Forestry, Franklin, South Africa	-30.3305	29.5184
S. grayii	PEM A13864	Mpur Forestry, Franklin, South Africa	-30.3305	29.5184
S. grayii	PEM A13870	Gomo Forest Stop 2, South Africa	-31.0102	29.3564
S. grayii	PEM A13871	Elandskuil Guest Farm, South Africa	-30.5206	29.6646
S. grayii	PEM A13881	Tower above Ingeli Forest, South Africa	-30.5216	29.6919
S. grayii	MHNG 2162.81	Giant's Castle National Park, Drakensberg, 2000 m, South Africa	-29.0887	29.3947

Species	Voucher	Locality	Latitude	Longitude
S. grayii	MHNG 2162.82	Giant's Castle National Park, Drakensberg, 2000 m, South Africa	-29.0887	29.3947
S. grayii	MHNG 2701.1	Sewefontein, South Africa	-32.5854	19.0039
S. grayii	MHNG 2701.2	Sewefontein, South Africa	-32.5854	19.0039
S. grayii	PEM A12228	Baviaanskloof, Bergplaas to Witte River Hike, South Africa	-33.6283	24.4623
S. grayii	PEM A5805	Mont aux Sources, South Africa	-28.6619	28.9993
S. grayii	PEM A5863	Strand, South Africa	-34.0946	18.8209
S. grayii	PEM A5885	Sabie, South Africa	-24.8911	30.7543
S. grayii	PEM A5886	Sabie, South Africa	-24.8911	30.7543
S. grayii	PEM A6421	Baardskeerdersbos, South Africa	-34.5875	19.5703
S. grayii	PEM A6895	Plettenberg Bay, Zenon street at Nature Conservation office, South Africa	-34.0347	23.3669
S. grayii	PEM A9072	Covie, near Nature's valley, South Africa	-33.9500	23.6017
S. grayii	PEM A9074	Nature's Valley, South Africa	-33.9761	23.5611
S. grayii	PEM A9542	Paapenkuils, Bridgemead, South Africa	-33.9241	25.4703
S. grayii	PEM A9664	Seal Point Nature Reserve, Cape St. Francis, South Africa	-34.2069	24.8186
S. grayii	PEM A963	Springbok, South Africa	-29.6800	29.6800
S. grayii	PEM A964	Springbok, South Africa	-29.6831	29.6831
S. grayii	PEM A965	Springbok, South Africa	-29.6831	29.6831
S. grayii	PEM A966	Springbok, South Africa	-29.6831	29.6831
S. grayii	PEM A967	Springbok, South Africa	-29.6831	29.6831
S. grayii	PEM A968	Springbok, South Africa	-29.6831	29.6831
S. grayii	PEM A15008	Studers Pass, South Africa	-30.4281	18.0616
S. merumontanus	MHNG 2619.86	Iringa, Udzungwa, Masisiwe, Tanzania	-8.2833	35.9000
S. merumontanus	MHNG 2699.29	Idete, Lukosi River, Tanzania	-8.1000	36.4833
S. merumontanus	PEM A14987	Kitetele, Mbeya Mountain, Tanzania	-8.8401	33.5331
S. merumontanus	PEM A14988	Kitetele, Mbeya Mountain, Tanzania	-8.8401	33.5331
S. merumontanus	PEM A14989	Kitetele stream. 1 km North, Tanzania	-8.8401	33.5331
S. merumontanus	PEM A14990	Ndumbe stream, Poroto mts, Tanzania	-9.0225	33.2122
S. merumontanus	PEM A14994	Mbizi Hill Forest Reserve, Tanzania	-7.8932	31.68
S. merumontanus	PEM A10547	Kitulo Plateau, Tanzania	-9.0772	33.8558
S. merumontanus	PEM A11185	Mabu Forest Summit Camp, Mozambique	-16.2968	36.3924
S. merumontanus	PEM A11186	Mabu Forest Summit Camp, Mozambique	-16.2968	36.3924
S. merumontanus	PEM A11187	Mabu Forest Summit Camp, Mozambique	-16.2968	36.3924
S. merumontanus	PEM A11352	Mt Namuli, Muretha Plateau, Mozambique	-15.3877	37.0434
S. merumontanus	PEM A11358	Mt Namuli, Muretha Plateau, near trap 1, Mozambique	-15.3877	37.0434
S. merumontanus	PEM A11359	Mt Namuli, Muretha Plateau, near trap 1, Mozambique	-15.3877	37.0434
S. merumontanus	PEM A11357	Mt Namuli, Muretha Plateau, Mozambique	-15.3881	37.0452
S. merumontanus	PEM A11650	Muretha Plateau camp, Mt Namuli, Mozambique	-15.3877	37.0434
S. merumontanus	ZMB 79033	Umbwe route, Mt Kilimanjaro, Tanzania	-3.1800	37.2800
S. merumontanus	ZMB 79034	Nkweseko, Mt Kilimanjaro, Tanzania	-3.1824	37.2426
S. merumontanus	ZMB 79035	Marango route, Mt Kilimanjaro, Tanzania	-3.2228	37.5146
S. merumontanus	ZMB 79036	Kidia Forest, Mt Kilimanjaro, Tanzania	-3.2803	37.4406
S. merumontanus	ZMB 79037	Mweka Dam, Mt Kilimanjaro, Tanzania	-3.2166	37.3425
S. merumontanus	CAS 225066	Kitumbeine Forest, Tanzania	-2.9000	36.23501
S. merumontanus	PEM A7499	Kitumbeine forest, Tanzania	-2.9044	36.2350
S. merumontanus	CAS 225065	Kitumbeine forest, Tanzania	-2.9044	36.2350
S. merumontanus	CAS 225066	Kitumbeine forest, Tanzania	-2.9044	36.2350
S. merumontanus	CAS 225067	Kitumbeine forest, Tanzania	-2.9044	36.2350

Species	Voucher	Locality	Latitude	Longitude
S. merumontanus	PEM A14991	Mt Meru, Tanzania	-3.2998	36.9366
S. merumontanus	PEM A14992	Mt Meru, Tanzania	-3.2998	36.9366
S. merumontanus	PEM A14993	Mt Meru, Tanzania	-3.2998	36.9366
S. rhodesianus	MHNG 1295.72	Gleneagles, Inyanga, Zimbabwe	-17.8700	30.9100
S. rhodesianus	PEM A2792	Mt Gorongosa, Mozambique	-18.5928	34.2421
S. rhodesianus	PEM A2793	Mt Gorongosa, Mozambique	-18.5928	34.2421
S. rhodesianus	PEM A6425	Chirinda Forest, Zimbabwe	-20.4193	32.6832
S. wageri	NMSA-HER-005343-D2	Weza Forest, Harding, South Africa	-30.6407	29.7450
S. wageri	NMSA-HER-005343-D5	Weza Forest, Harding, South Africa	-30.6407	29.7450
S. wageri	NMSA-HER-005980	Qudeni, South Africa	-28.6077	30.8650
S. wageri	NMSA-HER-006409	Lundy's Hill, South Africa	-29.7256	29.9370
S. wageri	NMSA-HER-006410	Lundy's Hill, South Africa	-29.7256	29.9370
S. wageri	NMSA-HER-006563	Bannerman Hut area, South Africa	-29.2514	29.4420
S. wageri	NMSA-HER-007330	Karkloof Nature Reserve, South Africa	-29.2999	30.2800
S. wageri	NMSA-HER-007352	Entumeni Nature Reserve, South Africa	-28.8889	31.4640
S. wageri	NMSA-HER-007353	Entumeni Nature Reserve, South Africa	-28.8889	31.4640
S. wageri	NMSA-HER-007356	Giant's Castle Game Reserve, South Africa	-29.3451	29.4820
S. wageri	NMSA-HER-007357	Giant's Castle Game Reserve, South Africa	-29.3451	29.4820

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New information on *Trichophiala devylderi* Aurivillius, 1879. Full description of both sexes, genetic study and lectotype designation (Lepidoptera, Eupterotidae)

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Abstract: Described from Namibia, *Trichophiala devylderi* Aurivillius, 1879 is a species for which, apart from the original description of female "types", little is known. Building upon recent observations in the field, investigations in various museums that preserve specimens, and a review of the literature, we describe for the first time the habitat, the known distribution, the morphology of both sexes including the presence of two phenotypes, and the genitalia of both male and female. We also provide genetic information from several specimens that reveal little variation in the standard animal DNA barcode. Finally, we designate a lectotype among the three specimens preserved at the Naturhistoriska Riksmuseet, Stockholm, Sweden.

Keywords: *Trichophiala devylderi* - Eupterotidae - Striphnopterygidae - moths - Namibia - Africa - Aurivillius - lectotype.

INTRODUCTION

Trichophiala devylderi Aurivillius, 1879 was described from Namibia as type species of the monotypic genus *Trichophiala* (Aurivillius, 1879). In a subsequent publication on the then family Striphnopterygidae, Aurivillius (1901) briefly re-described the species in English after having used Latin in the original 1879 report. The species belongs to the family Eupterotidae Swinhoe, 1892, and was included in the subfamily Striphnopterigynae Wallengren 1858 in the recent checklist of the Bombycoidea (Insecta: Lepidoptera) by Kitching *et al*. (2018). Although described over 140 years ago, *Trichophiala devylderi* is poorly known.

Building on field observations in Namibia in 2017, subsequent literature searches and investigations in museums, we review the available information, present a distribution map based on all known records, provide a complete description of the male of this species, describe the genitalia of both sexes for the first time, note the presence of two morphologically distinct phenotypes, and report limited genetic variation among individuals from the analysis of the standard animal DNA barcode (Hebert *et al.*, 2003). In addition, we demonstrate the need for a lectotype to be designated and proceed with its designation among three available syntypes. Finally, we propose a list of research objectives that would enhance the overall knowledge of the species.

METHODS

In August 2017 one of us (MR) spent time in Namibia and on two occasions (8 August and 21 August) stayed overnight at a lodge some 5 km east of the capital, Windhoek. During both evenings, starting at around 8 p.m. dozens of individuals of a light brownish moth appeared around the lamps of the lodge. The following mornings, a few individuals were still observed on the walls near the lamps but disappeared almost completely around 09h00. Seven specimens (six males and one female) were collected and later prepared for analysis. They were eventually identified by one of us (VZ) as *Trichophiala devylderi* Aurivillius, 1879 (Eupterotidae).

Given the scarcity of information on this species, a thorough literature search was undertaken exploring articles,

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books and internet sites related to African moths and the family Eupterotidae using the following keywords or combinations: *Trichophiala devylderi,* Eupterotidae, African moths, Namibian moths, South African moths, Aurivillius, De Vylder.

The site Biodiversity Heritage Library (biodiversity-library.org) was extensively consulted for older publications.

Several large natural history museums and moth experts were contacted to gather information on the species and on additional specimens available. Besides the Muséum d'histoire naturelle (MHNG) of Geneva, the Swedish Museum of Natural History (NHRS or Naturhistoriska Riksmuseet, Stockholm), and the Muséum national d'Histoire naturelle (MNHN) of Paris, these included: Dr Wolfram Mey of the Museum für Naturkunde (MNB), Berlin, Germany; Dr Ole Karsholt of the Natural History Museum of Denmark in Copenhagen, Denmark; Dr Alessandro Giusti of the Natural History Museum, London, U.K; and Dr László Ronkay, Budapest, Hungary. The following natural history museums were also contacted to enquire about the possible presence of specimens: Zoologische Staatsammlung Munich, Germany (ZSM); Museum Thomas Witt, Munich, Germany (MWM); and Senckenberg Museum, Frankfurt, Germany (SMF). Additionally, natural history museums of the African sub-region where *T. devylderi* is found were also contacted. They included the Museums Association of Namibia, Windhoek, Namibia, the Iziko Museums in Cape Town, South Africa, and the Ditsong National Museum of Natural History in Pretoria (DNMNHP), South Africa.

The platform iNaturalist was consulted. Finally, prompted by Mr Jeremy Dobson, in January 2018 the Lepidopterists' Society of Africa issued a call to its members for information on the species through the African Butterflies News, January/February 2018 (Dobson, 2018).

The morphological description is based on the analysis of several specimens preserved at MWM, ZSM (4 males and one female) and three specimens of both sexes preserved at MHNG that were studied using techniques including dissection of the genitalia of eight specimens. The wing pattern is described based on specimens available in MHNG, MNB, and NHRS.

Genetic analyses were carried out in the molecular biology laboratory SSM ("Service de Systématique Moléculaire", UMS2700) at MNHN, Paris. We sampled a single leg from each of 12 recently collected specimens [between 2008 and 2017; vouchers deposited in MWM (6), MHNG (3) and MNB (3)] representing light and dark forms (see below) originating from five different sites in Namibia. Each leg went through DNA extraction using a Macherey-Nagel NucleoSpin® 96 tissue kit, and following the manufacturer's protocol, applying a semi-automated procedure implemented on an Eppendorf Liquid Handling Workstation epMotion® 7075 VAC. PCR amplification and sequencing followed the high-throughput protocol described in Sire *et al*. (2019), except for the use of primer pairs LCO1490/MLepR1 and MLepF1/HCO2198 (Folmer *et al*., 1994; Hajibabaei *et al.,* 2006). This approach uses a dual-indexing multiplexing strategy for library construction and sequencing on the Illumina MiSeq platform. We used Geneious R10 (https:/www.geneious.com) for filtering, cleansing, assembling and aligning the paired-end reads produced with this approach. We also processed at SSM one of the original syntypes of *T. devylderi* preserved at NHRS; because this specimen was collected in the second half of the 19th century, we used a dedicated laboratory protocol targeting shorter DNA fragments as in Hausmann *et al*. (2009). DNA was extracted using DNeasy extraction kits (Qiagen) for blood and animal tissues and then amplified using six different primer pairs as described in Lees *et al*. (2010). PCR products were deposited on 2% agarose gel, checked under UV light and only successfully amplified DNA templates were sent for Sanger sequencing on ABI 3730XL sequencer at Eurofins MWG Operon sequencing facilities (Ebersberg, Germany). We used Geneious R10 for contig assembly, editing and alignment. All consensus sequences obtained were uploaded into BOLD (www.boldsystems.org) along with other specimen information (taxonomy, voucher depository, sex, and collecting data) and images. Complete records and GenBank accession numbers are publicly available from dataset DS-TRICHO21 (DOI: dx.doi.org/10.5883/DS-TRICHO21), along with those of four additional DNA barcoded records kindly made available to us by Thierry Bouyer. Genetic distances were computed using analytical tools implemented in BOLD (Ratnasingham & Hebert, 2007), using uncorrected p-distances.

RESULTS

History of the description of *Trichophiala devylderi*

Trichophiala devylderi was described by the Swedish entomologist Per Olof Christopher Aurivillius in 1879 (Aurivillius, 1879). The original publication in Latin first described the main features of the family Phialidae (today known as Eupterotidae) (Nässig & Oberprieler, 2007) and of the new genus *Trichophiala* established to accommodate the new species (pp. 53-54), signalling its connection to the genus *Phiala* Wallengren, 1860, but distinguishable on the basis of antennae, tibiae, and a few other details. This was followed by a short description of the female types of the new species (Fig. 1). Later, Aurivillius (1901) re-described the species (p. 14 and pl. 3) as part of a review of the family that had become known as Striphnopterygidae presenting an image of the female (Fig. 1).

Aurivillius described the new species based on female specimens collected in Namibia by the Swedish naturalist

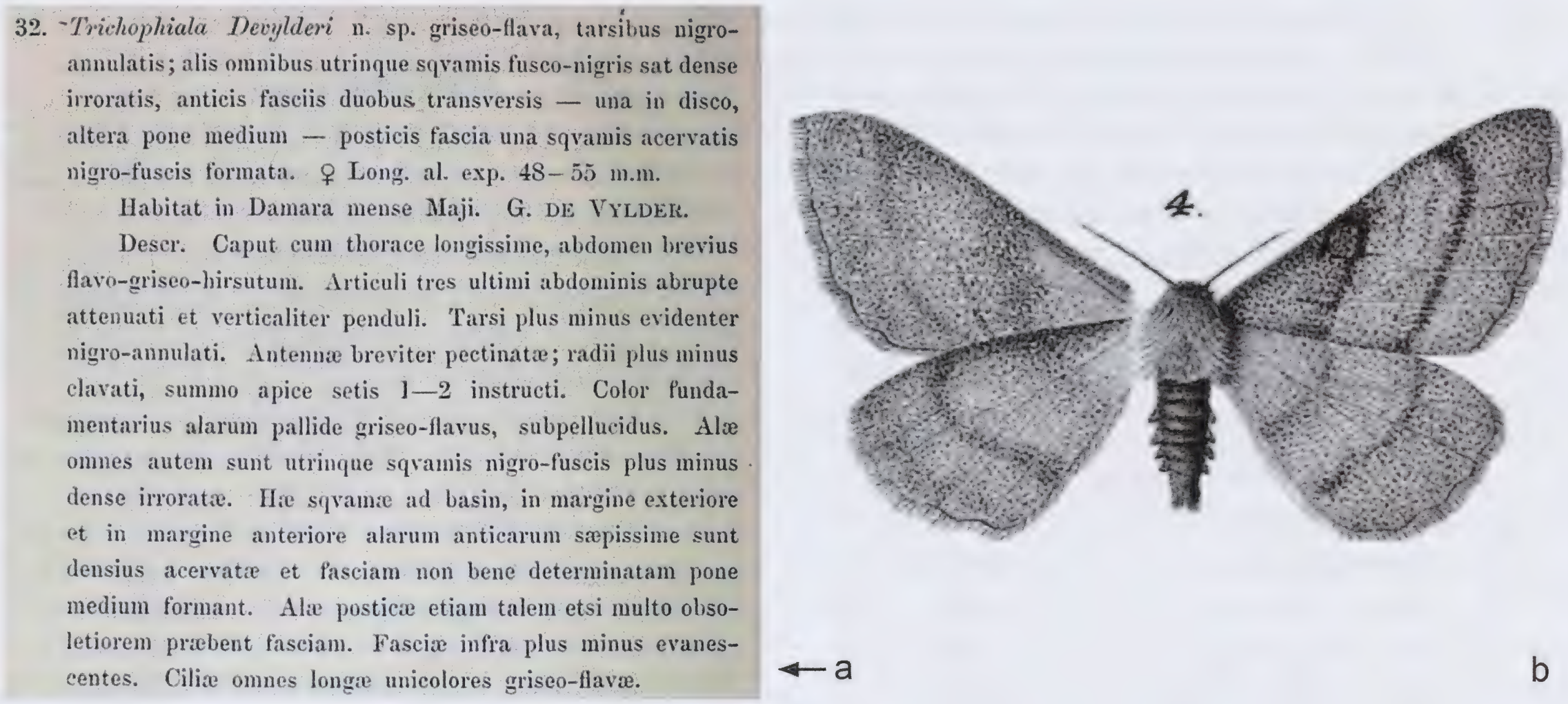

32. *Trichophiala Devylderi* n. sp. griseo-flava, tarsibus nigro-annulatis; alis omnibus utrinque sqvamis fusco-nigris sat dense irroratis, anticis fasciis duobus transversis — una in disco, altera pone medium — posticis fascia una sqvamis acervatis nigro-fuscis formata. ♀ Long. al. exp. 48–55 m.m.
Habitat in Damara mense Maji. G. DE VYLDER.
Descr. Caput cum thorace longissime, abdomen brevius flavo-griseo-hirsutum. Articuli tres ultimi abdominis abrupte attenuati et verticaliter penduli. Tarsi plus minus evidenter nigro-annulati. Antennæ breviter pectinatæ; radii plus minus clavati, summo apice setis 1—2 instructi. Color fundamentarius alarum pallide griseo-flavus, subpellucidus. Alæ omnes autem sunt utrinque sqvamis nigro-fuscis plus minus dense irroratæ. Hæ sqvamæ ad basin, in margine exteriore et in margine anteriore alarum anticarum sæpissime sunt densius acervatæ et fasciam non bene determinatam pone medium formant. Alæ posticæ etiam talem etsi multo obsoletiorem præbent fasciam. Fasciæ infra plus minus evanescentes. Ciliæ omnes longæ unicolores griseo-flavæ.
4.
a
b

Fig. 1. (a) Original 1879 description of *Trichophiala devylderi* Aurivillius, 1879; (b) first image of the new species published by Aurivillius in 1901.

Gustaf De Vylder (1827-1908) either in 1873 or 1874. Three of them are preserved at NHRS and one at MNB (see Table 1). One of these specimens is labelled "Type" by Aurivillius.

De Vylder spent three years in southern Africa, financed by the Swedish Government on the condition of collecting natural history specimens for Swedish museums. After leaving Sweden in the summer of 1871, De Vylder reached Cape Town in November of that year, following a long journey through Madeira, the Azores, St. Vincent and Rio de Janeiro. In March 1873, he finally reached Port Nolloth and, from there, the territory of today's Namibia. During the years 1873-1874, he collected a large number of entomological specimens, including in the region at the time called Damaraland (Damara being synonymous with Herero, one of the ethnic groups of Namibia), and Damaraland being the territory in the north-central part of what later became Namibia, comprised between the Swakop River and the Windhoek area in the south, the Ugab River and the Ovamboland in the north, the Namib Desert in the west, and the northern part of the Kalahari Desert in the east. His diary (Rudner & Rudner, 1998) describes in detail his long journey and his work methods, but does not refer directly to the observation and collecting of the moths described by Aurivillius. Upon De Vylder's return to Sweden in 1874, the moths were made available to the NHRS and Aurivillius.

Literature review

Several articles were identified that mentioned the species. Besides the 1879 and 1901 descriptions by Aurivillius, the consultation of the site Biodiversity Heritage Library (biodiversitylibrary.org) yielded several citations of the species in general lists of moths, especially during the period 1880-1917, with no description. These include a 1910 mention of three females and one undefined specimen collected at three different locations of today's Namibia (Grünberg, 1910). In 1930, in the book by A. Seitz "Die Gross-Schmetterlinge der Erde", M. Gaede provided a morphological description of the species (Gaede, 1930). He wrote the following (translated from German):

"Palps short. Antennae of male as in *Lichenopteryx,* in female with only short pectination. Fore tibiae with 2 spurs. Veins on forewings rather straight. Vein 5 close under upper corner, veins 6 + 7 + 8 + 9 + 10 stalked. In hindwings vein 5 far forward, veins 6 + 7 pedunculate, vein 8 only in male anastomosing with the cell groove, in the female connected with it by a bar. Adhesive bristle present in male, absent in female. Thorax dark brownish grey. Wings greyish yellow, brown sprinckled and with four bands on forewings: 2 broader ones parallel, 2 weaker ones in between. Margin darkly sprinckled, especially on the upper surface very broad and rather sharply defined. Abdomen orange-brown. 50-55 mm. South-West Africa".

For the first time Gaede mentioned three features of the male. They seem to be similar, if not identical, to those of several Eupterotidae, in particular some species of the genus *Lichenopteryx* and, to some extent, *Phiala, Poloma,* and *Phillalia.* The three features described are quite similar to what was already reported in Aurivillius (1901) for Striphnopterygidae. Seitz's book also presents

Table 1. List of specimens of *T. devylderi* preserved in different collections or reported in published materials. n.a. = not available; (DMNG) = from Grünberg (1910) in Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena; RCTB = Research Collection of Thierry Bouyer, Chênée, Belgium; N = convenience numbers for further reference. Note: Most specimens belong to the sandy-gray form; specimens 11, 12, 18, 33, 34, 72, 78, 79 belong to the darker pinkish-brown form – see below.

N	Site	Country	Sex	Date	Leg.	Collection
1-3	Damara	Namibia	3♀	6/5/?1873	De Vylder	NHRS
4	Damara	Namibia	1♀	6/5/?1873	De Vylder	MNB
5	Damaraland	Namibia	n.a.	n.a.	n.a.	(DMNG)
6-7	Windhoek	Namibia	2♀	n.a.	Lindt	(DMNG)
8	Windhoek	Namibia	1♂	n.a.	Zobrys	MNB
9-10	Windhoek	Namibia	2♀	n.a.	Lindt	MNB
11-14	Windhoek	Namibia	3♂ 1♀	VI, VIII	n.a.	DNMNHP
15-18	Windhoek	Namibia	4♂	1/7/1998	G. Betti	RCTB
19-25	Windhoek Auas Berge	Namibia	7♂	26/4/2000	Burmeister	ZSM
26-32	Korlia vicinity	Namibia	6♂ 1♀	8-21/8/2017	Raviglione	MHNG
33-45	Okahandja	Namibia	8♂ 5♀	I, V	n.a.	DNMNHP
46	Okahandja	Namibia	1♂	17/5/1955	n.a.	SMF
47	Grootfontein	Namibia	1♂	IX	n.a.	DNMNHP
48-51	Abachaus	Namibia	3♂ 1♀	v,vi,vii	n.a.	DNMNHP
52	Portsmut	Namibia	1♂	VI	n.a.	DNMNHP
53-61	Farm Valencia 42	Namibia	9♂	IV, VI	n.a.	DNMNHP
62	Omuweroumue	Namibia	1♀	n.a.	Seewald	MNB
63	Khomas, Farm Vaalgras	Namibia	1♂	21/9/2008	F. Koch	MNB
64-71	Otjiwarongo	Namibia	8♂	25-27/7/2012	W. Mey	MNB
72	Otjiwarongo	Namibia	1♂	4/8/2010	N. Pürzer & C. Ganslmeier	MWM
73	Waterberg	Namibia	1♀	22/5/1909	Seewald	(DMNG)
74-79	Outjo Umg. Karanjab	Namibia	6♂	15/7/2010	W. Struijlaart & K. Lisbrand van der Meer	MWM
80-87	Bushcamp Umg. Khomas	Namibia	7♂ 1♀	31/8/2010	W. Cave & T. A. Newtown-Chance	MWM
88	Livingstone (8 ml N)	Zambia	1♂	25-28 V 1954	A.J.T. Janse	DNMNHP
89-90	Victoria Falls Camp	Zimbabwe	2♂	3-4- V 1954	A.J.T. Janse	DNMNHP

an image of the female of *T. devylderi* (Fig. 2). However, twenty-five years after Seitz's publication, Forbes still refers to the male of *T. devylderi* as unknown (Forbes, 1955). No description of the genitalia of either sex is available from the literature. The book by Pinhey on Southern African moths does not record the species (Pinhey, 1975), nor does the monograph on the Lepidoptera of the Brandberg Massif in Namibia (Mey, 2004, 2007).

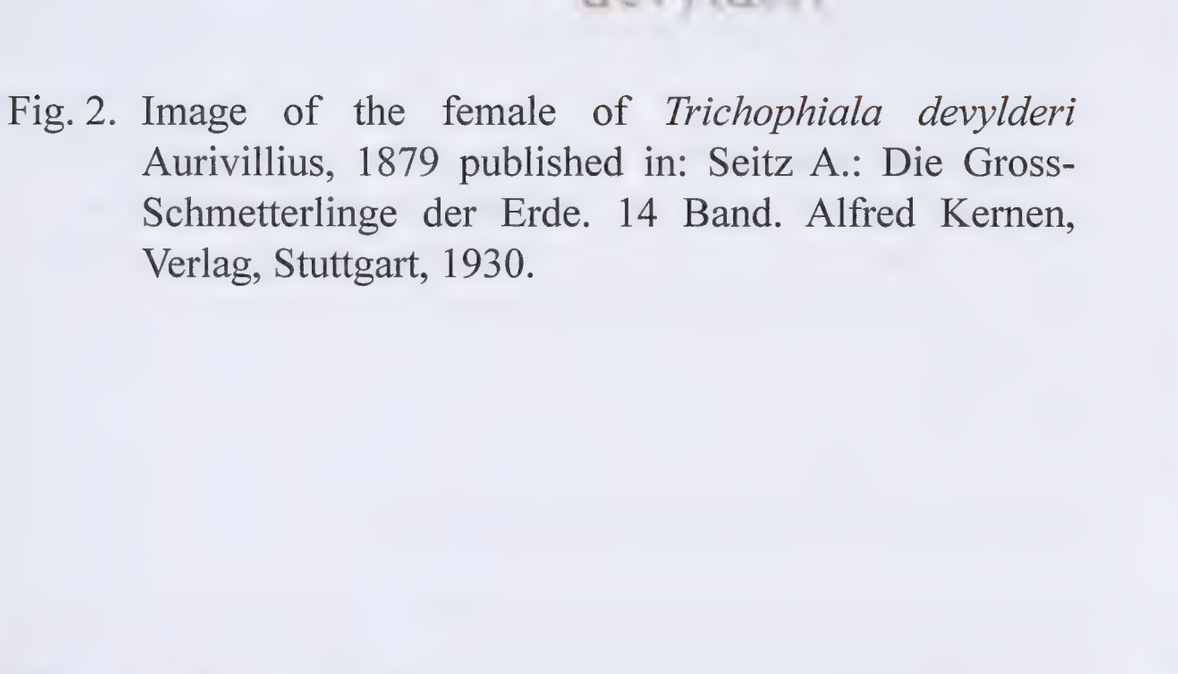
One photograph of one of the type specimens was found on two websites. The photograph is of a specimen hosted by the NHRS, where three of the type specimens are preserved (Naturhistoriska Riksmuseet, 2021). Besides the NHRS website, the same image is shown on AfroMoths, a website providing an extensive online database on Afrotropical moth species (De Prins & De Prins, 2011-2021); however, this website also shows males erroneously identified as *T. devylderi* that belong to other Eupterotidae species, presumably of the genus *Phiala*. The website "Lepidoptera and some other life forms" (Savela, 1990-2021) lists the species, but provides no additional information. The platform iNaturalist has no observation of *T. devylderi* (iNaturalist, 2011-2021) as of the month of January 2022. Finally, the Barcode of Life Datasystems (BOLD; www.boldsystems.org; Ratnasingham & Hebert, 2007) hosts four records of that species sampled from the research collection of Thierry Bouyer (Chênée, Belgium).

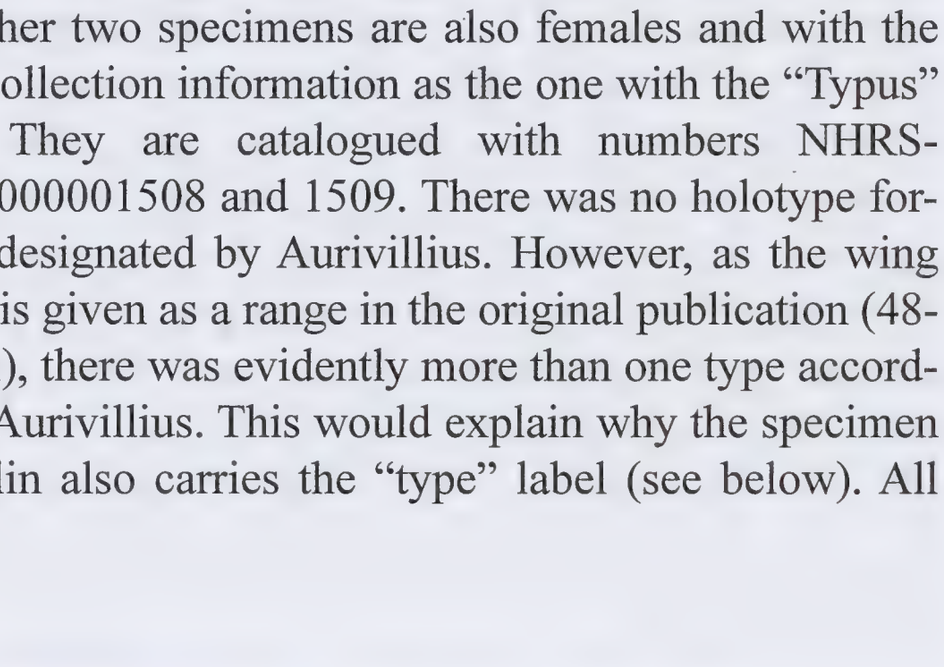
Fig. 2. Image of the female of *Trichophiala devylderi* Aurivillius, 1879 published in: Seitz A.: Die Gross-Schmetterlinge der Erde. 14 Band. Alfred Kernen, Verlag, Stuttgart, 1930.

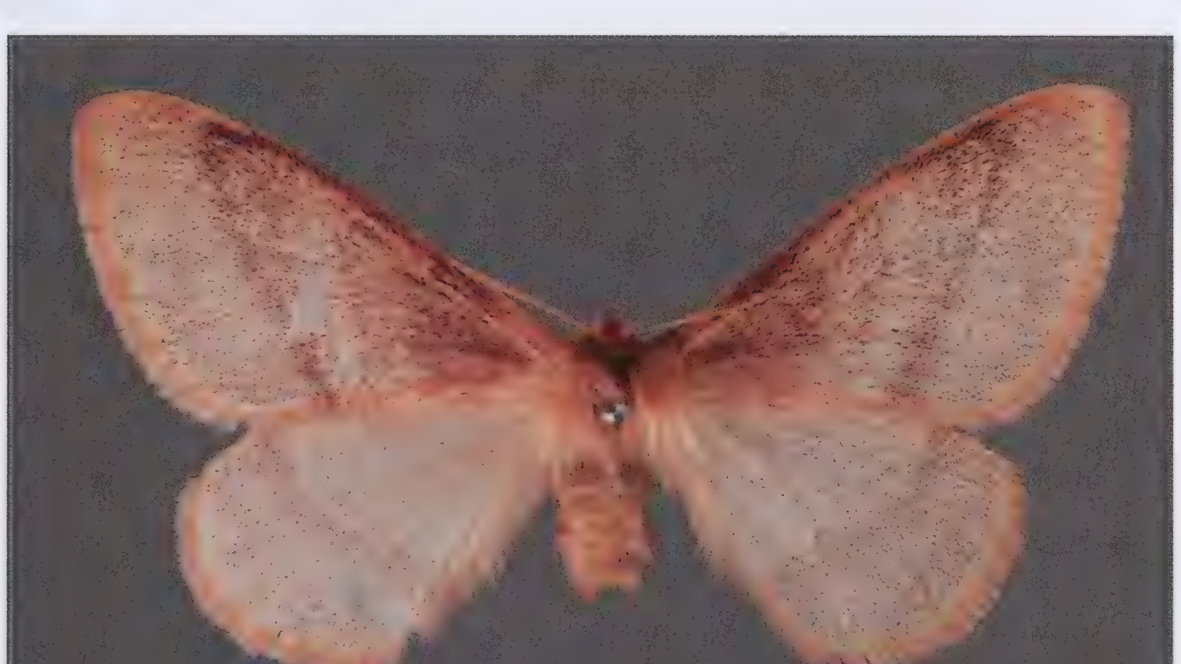
Existing *Trichophiala devylderi* types

The number of specimens collected as part of the initial De Vylder's series is unknown. As mentioned, at the NHRS there are currently three female syntypes of *T. devylderi* (Fig. 3). One additional original female syntype is preserved at the MNB (see below). Among the three specimens in the NHRS, there is one designated as "Typus". It is catalogued with the number NHRS-SRAH000001507 and corresponds to the specimen illustrated on the NHRS website, the only available internet image of the species: *Trichophiala devylderi Aur. Typus – Damara 6/5 - G. de Vylder*.

The other two specimens are also females and with the same collection information as the one with the "Typus" label. They are catalogued with numbers NHRS-SRAH000001508 and 1509. There was no holotype formally designated by Aurivillius. However, as the wing length is given as a range in the original publication (48-55 mm), there was evidently more than one type according to Aurivillius. This would explain why the specimen in Berlin also carries the "type" label (see below). All







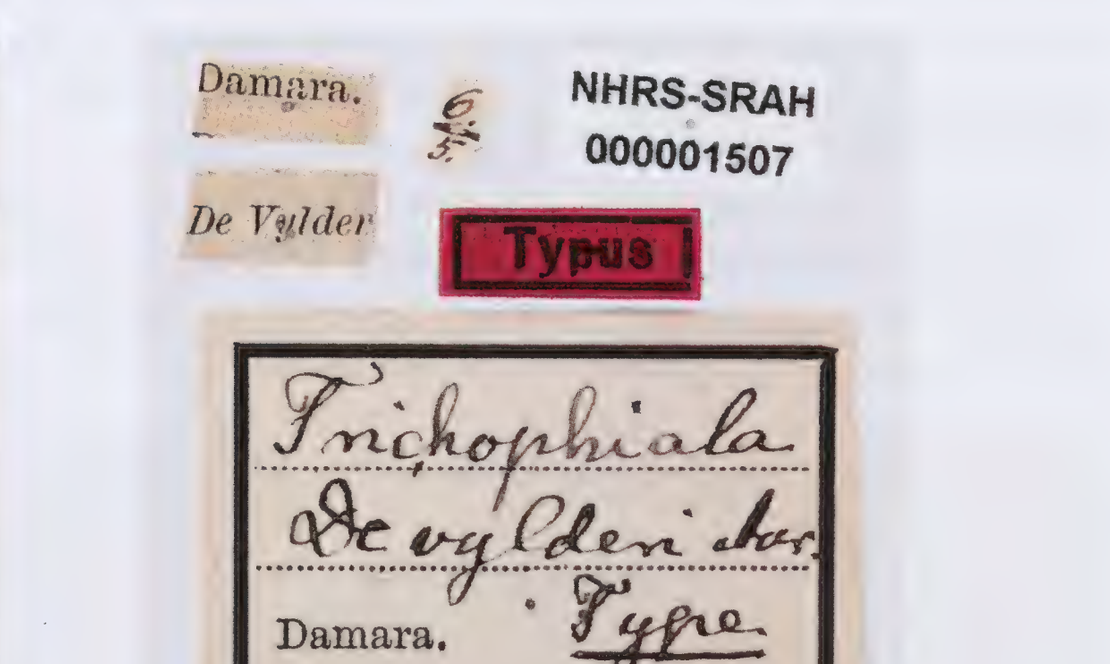


Fig. 3. The three syntypes of *T. devylderi* from the collection of the Stockholm Naturhistoriska Riksmuseet, (a) specimen NHRS-SRAH000001507 and (b) its original labels by De Vylder and the label "Typus", (c) specimen NHRS-SRAH000001508, (d) specimen NHRS-SRAH000001509.

three specimens at the NHRS should be considered as belonging to the type series (syntypes); they share the data "Damara", "6/5", "De Vylder". The additional syntype in the MNB (Wolfram Mey, pers. comm.), also a female, is registered with the following information: Type: 1 ♀, [Namibia], "Damara" [printed], "De Vylder" [printed], "32502" [printed], "6.5.", "*Trichophiala/devylderi* Typ." [handwritten with black ink on white paper].

Other specimens in museum collections

Among the consulted museums, only the Ditsong Museum in Pretoria, the MNB, ZSM, MWM, and SMF preserve specimens of *T. devylderi.* The specimens kept in those collections are presented in Table 1. In addition, there is information on some specimens cited by Grünberg in Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena (1910). These specimens are from Damaraland (one), Windhoek (2 females) and Waterberg, South Africa (one female, Seewald, 22 May 1909). Finally, the call for information through the Lepidopterists' Society of Africa did not yield any results.

***Trichophiala devylderi* distribution**

The distribution of *T. devylderi* is only partially known (Fig. 4). There is no information on the website AfroMoths (De Prins & De Prins, 2011-2021) while the Funet website (Savela, 1990-2021) reports generically "Namibia". Based on the data available from the specimens in the various collections (see Table 1), the distribution map of the species shows that it is present in several localities of Namibia, and, as far as other countries are concerned, it has been observed in May 1954 near Victoria Falls on both the Zambian and Zimbabwean sites.

Fig. 4. Distribution map of known sites of observation of *Trichophiala devylderi* (red dots: recent observations after 2000; blue dots: previous observations mostly from the late XIXth and early XXth century).

Habitat, flight period and life history

Little is known of the biology of *T. devylderi*. The original description only indicates the site where the specimens were collected. It then adds "month of May", which may correspond to the "6/5" (presumably 6th of May) on one of the original labels at the NHRS. Based on observations by one of us (MR) in the month of August 2017, the species lives in a habitat that is part of the highland shrubland of Namibia, at an altitude of approximately 1750 m, some 10 km east of Windhoek near Korlia (Fig. 5). The vegetation in the arid hilly area consists mainly of sparse shrubs and various *Acacia* species, with kudu bush (*Combretum apiculatum* Sond.) (Combretaceae) and buffalo thorn (*Ziziphus mucronata* Willd.) (Rhamnaceae).

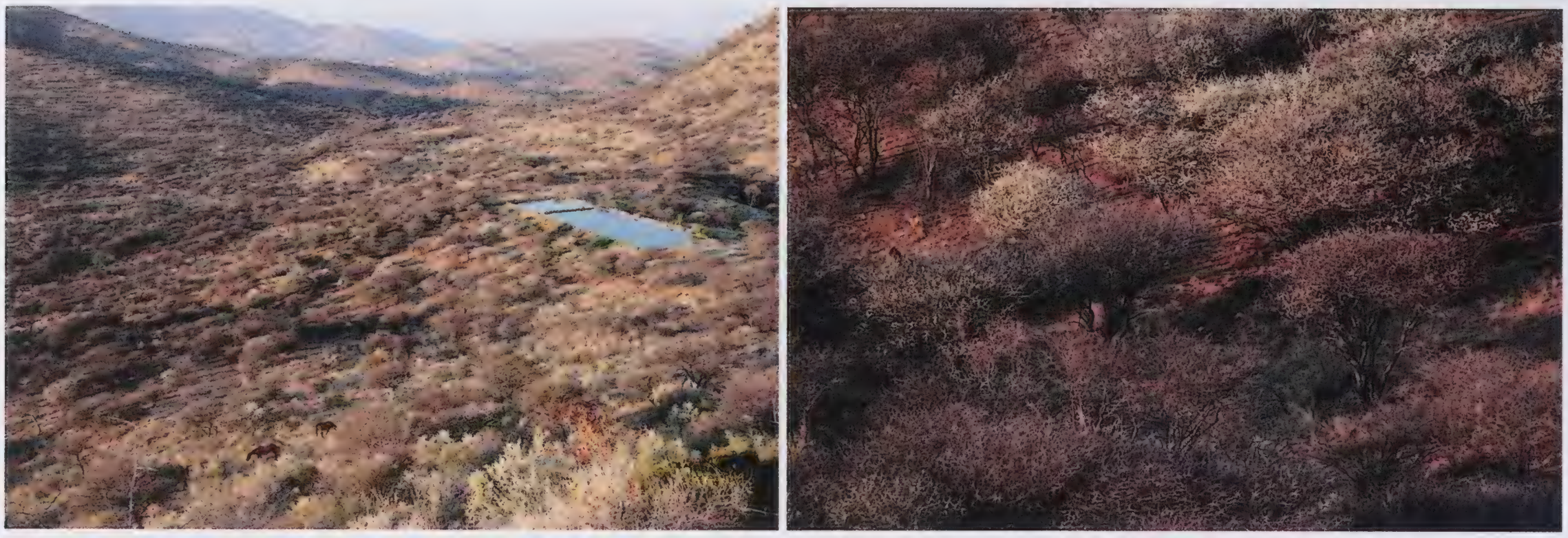


Fig. 5. Habitat of *T. devylderi* near Korlia, east of Windhoek, altitude 1750 m.

The flight period of the species has not been elucidated thus far. However, the available specimens in the various collections have been caught with maximum frequency around the austral cold and dry season in Namibia (from April to September, with a single isolated record each for the months of November and January). Therefore, one could conclude that the moth flies mainly during the austral winter.

The life history is largely unknown. The only available mentions of the larval stages are from few published articles, two of which focused on topics other than Lepidoptera. Gaerdes (1962) reported that in the past the "hairy caterpillars" of "a grey moth (*Trichophiala devylderi*)… when the acacias had been stripped bare, caused a lot of damage to garden trees". Jensen & Clinning (1974) mentioned that the "hairy caterpillars… were still abundant on the acacias" in early March 1974. Finally, another article only mentioned, in a broad comparison of genus *Trichophiala* with another species, the presence of "free larval procoxae like in Lasiocampoidea" (Oberprieler & Duke, 1994). There is however no full description of the morphology of the immature stages of *Trichophiala*. The adult is highly phototropic as observed during the month of August 2017 when hundreds of individuals were coming to the lights of a lodge starting at sunset at around 8 p.m. and probably throughout the night (Fig. 6a-b). A few individuals were still present on the walls near the lights in the early morning (Fig. 6c), but the vast majority was gone after dawn.

Redescription of imago with revision of the female and first complete description of the male

Due to the limited original description available for this species, the female is re-described and a full description of the male is provided for the first time.

Trichophiala devylderi Aurivillius, 1879, Öfversigt af Kongl. Vetenskaps-Akademiens Forhandlingar 36 (7): 54. Type locality: "in Damara," Namibia.

Male (Fig. 7). Head small, with short labial palpus and large eye. Antenna bipectinate, as long as ca 2/5 of costal margin of forewing, pale creamy yellow; pectination longest at middle of flagellum, as long as about 8x width of corresponding flagellomeres. Head and thorax with mostly uniform yellowish sandy hair-like cover dorsally and ventrally, also with dark brown hair-like scales around labial palpi and below head, between forelegs. Coxa and femur of all legs with long, sandy, hair-like scales, particularly prominent on hindleg; tibia dorsolaterally with long, hair-like scaling, slightly darker than on femur, earth yellow, with few dark brown scales; tarsomeres with simply pointed or apically bifid thin and slightly elongate scales, earth yellow to orange with dark brown at their bases. Wingspan 41-47 mm, forewing length 22-26 mm. Forewing with weakly pointed apex, with widely rounded outer margin, of sandy ground colour, with admixture of brown to rusty-brown cover scales which can be grouped in certain fields, in which case they form darker zones, most typical among them a submarginal field and shadow-like fasciae medially; pattern consisting of two medial fasciae rather distinct in all

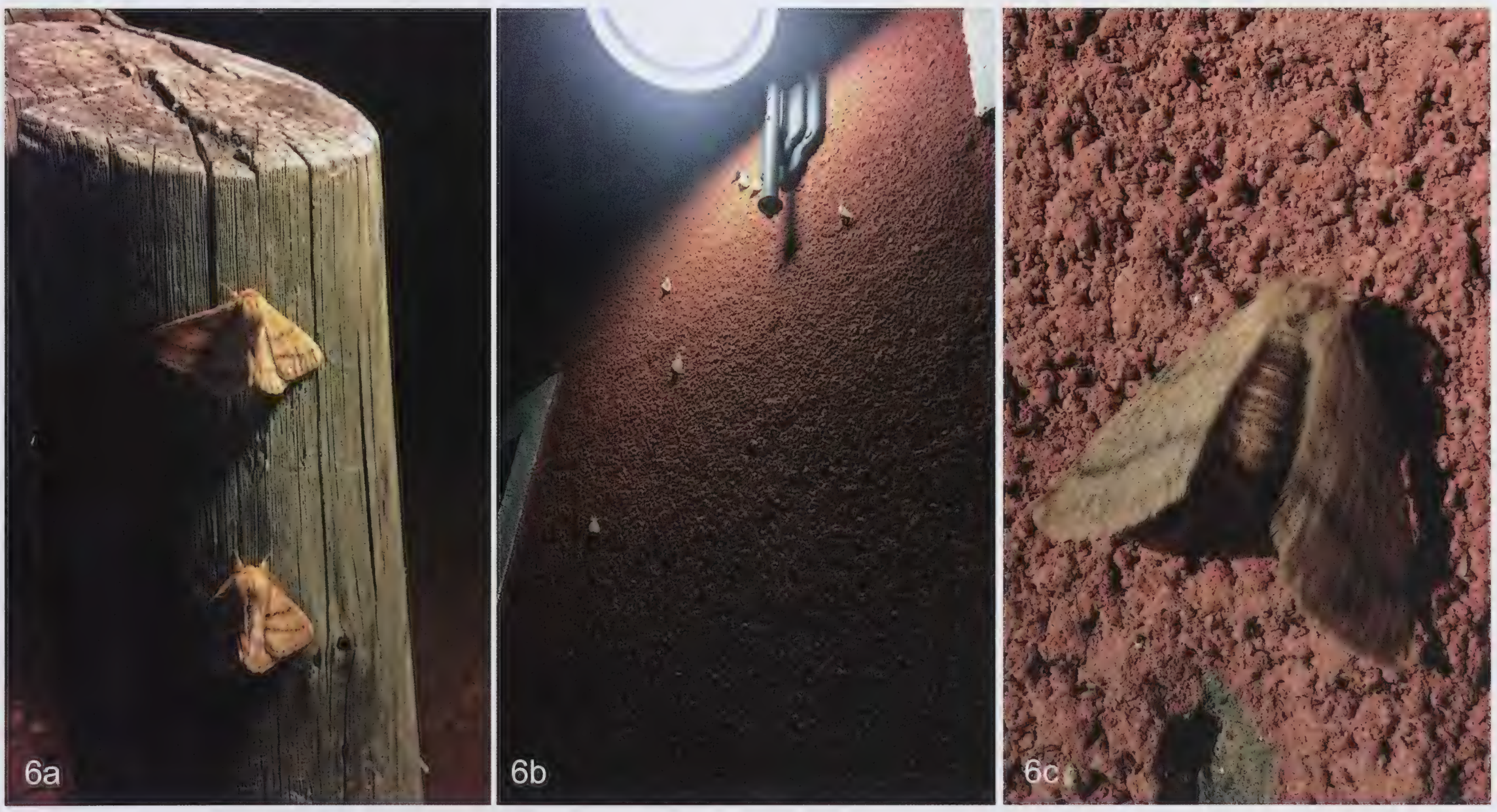


Fig. 6. (a-b) Individuals of *T. devylderi* flying to the light during the evening, (c) female still resting on the wall near a light in the early morning hour. Vicinity of Korlia, Namibia, August 2017.

Fig. 7. A male of *T. devylderi* (a) dorsal view, (b) ventral view. Vicinity of Korlia, Namibia, August 2017.

specimens as diffuse but obvious transversal post-medial and antemarginal bands; antemarginal fascia 7-shaped and antemarginal slightly curved, S-shaped; without basal band and discal dot/spot; fringe often paler and visible in contrast with darker submarginal field, sandy coloured, with narrow darker strokes on tips of veins. Hindwing with rounded outer margin, of same ground colour as forewing, with both fasciae very faint; submarginal field often darkened with greyish or reddish-brown scales; fringe uniformly sandy yellow.

In addition to typically coloured forms, darker individuals can be found (Fig. 8); they are rust brown, with very narrow elements of forewing pattern, contrasting dark fringe on both wings, but with reduced dark suffusion on hindwing.

Abdomen long and slender, with long hair-like, sandy yellow cover scales apically forming a tuft around last segment and shorter, darker, undercover spine-like pointed scales more strongly fixed on integument of tergites 1-8.

Male genitalia (Figs 9-10). Small and highly modified. Tergites without setae; tergum 10 membranous except for pair of medially separated plates enlarged medially and laterally, and smaller median triangular plate at base; tergum 9 (tegumen) reduced to narrow weakly sclerotized band medially widened and slightly projecting as triangle anteriorly. Vinculum very narrow, medially projected posteriorly as triangle with more thickly sclerotized margins; with very long saccus, as long as length of genital capsule, very slender basally, 3-5 times broader distally. Valva with swollen basal section and 'bird-head-like' distal valvula; basal section medially most thickly sclerotized, corrugated, and with thick cover of short setae, elsewhere with very sparse short setae, apparently fused with vinculum along basal margin; valvula with setae of variable lengths, mostly laterally and ventrally, with some quite long at apex. Juxta sheath-like, quadrangular in lateral view, with ventral edge and lateral margins slightly more strongly sclerotized. Phallus rather short, slightly longer in darker phenotype; without coecum; shaft slightly down-curved, wider at base and apex, slenderer in darker phenotype, opening directly caudad, ventrally before apex with short, rounded projection; vesica small, without cornuti or scobination.

Female (Fig. 11). Head with antennae bipectinate, with pectination very short, as long as ca. 1/3 of costal margin of fore wing, pale creamy yellow. Head and thoracic colouration as in male. Wing pattern and coloration generally corresponding to those of sandy coloured males, but more diffuse and rougher; no darker females are known. Cilia more yellowish than in males. Individual variation is visible in development of grey-brownish suffusion on wings and prominence of wing pattern elements. Wingspan 49-54 mm, forewing length 27-30 mm. Foreleg and midleg as in male, with more dark brown hair-like scales on foretibia in available specimen; hindleg unavailable for description. Abdomen rather robust; tergites with long, hair-like and short, trifid whitish sandy cover scales and with short and thin, spine-like pointed ochre undercover scales on most of surface more strongly affixed to integument, as in male, also with tuft of longer pale ochre hair-like scales apically; ventrally more uniformly coloured with pale ochre to whitish mostly narrow scales of medium length.

Female genitalia (Figs 9, 12). Papillae anales short, ovoid, weakly sclerotized, covered with setae longer dorso-apically. Apophyses posteriores and anteriores very slender; posteriores about 1/5 shorter than anteriores, connected to narrow sclerotized band around base of segment except ventrally; anteriores connected to slightly wider narrow sclerotized band enlarging laterodorsally but not connected dorsally, moderately setose except ventrally where it forms an arc with the posterior margin blunt medially, also with small unsclerotized oval window in sclerotized band at level of base of each apophysis anterioris. Ostium bursae medially situated, behind sclerotized band of sternite VIII. Antrum short, wide, wrinkled and not sclerotized. Ductus bursae short and narrow, unsclerotized, about as long as segments

Fig. 8. Specimens of *Trichophiala devylderi* preserved at MWM. The three male specimens on top left column show a pattern (darker rusty-pinkish-brown colour) that differs from that of the majority of the other, sandy ground-coloured, males..

Fig. 9. Male genitalia (first 4 on left) and female genitalia (far right) of *Trichophiala devylderi* shown with the image of the corresponding individual (on top). The first two males on left show the darker phenotype (specimens from MWM).

8-10, forming right angle for short distance before connecting with oviduct, with short tube before right angle connected to small (about as long as ductus seminalis) pear-shaped corpus bursae devoid of sclerotization. Paired glandulae sebaceae very long, connected by short tube to oviduct.

DNA barcode analysis: genetic variation in *Trichophiala devylderi*

Pairwise comparisons of the 16 full-length (658bp) DNA barcode sequences obtained from the recently collected specimens revealed nearly no genetic variation for this marker within this species (mean p-distance = 0.13%; maximum p-distance = 0.32%). Dark individuals share identical DNA barcodes with the lighter ones; this supports the interpretation of these variations in habitus as being mere individual forms of a single species. The short DNA sequence of 126bp recovered from the syntype of *T. devylderi* proved strictly identical, over its length to 11 of the 16 sequences obtained from the recent specimens. DNA barcodes of *T. devylderi* cluster as BIN BOLD:AAP1066 (as of January 19th, 2022) in BOLD's automated DNA-based registry (Ratnasingham & Hebert, 2013). Its nearest neighbour is *Teratojana flavina* Hering, 1937 of the Striphnopteryginae subfamily, with a minimum p-distance between the two species of 5.13%.

Lectotype designation

The two phenotypical forms observed in *Trichophiala devylderi* show some degree of genital differentiation. Pending future insights into this issue, these differences warrant the designation of a lectotype from the three syntypes in the NHRS. Therefore, we designate the more elaborately labelled female held at NHRS (NHRS-SRAH000001507) as lectotype for the species (Fig. 3). The other two females held at NHRS as well as the female from the original collection by De Vylder held at MNB become therefore paralectotypes.

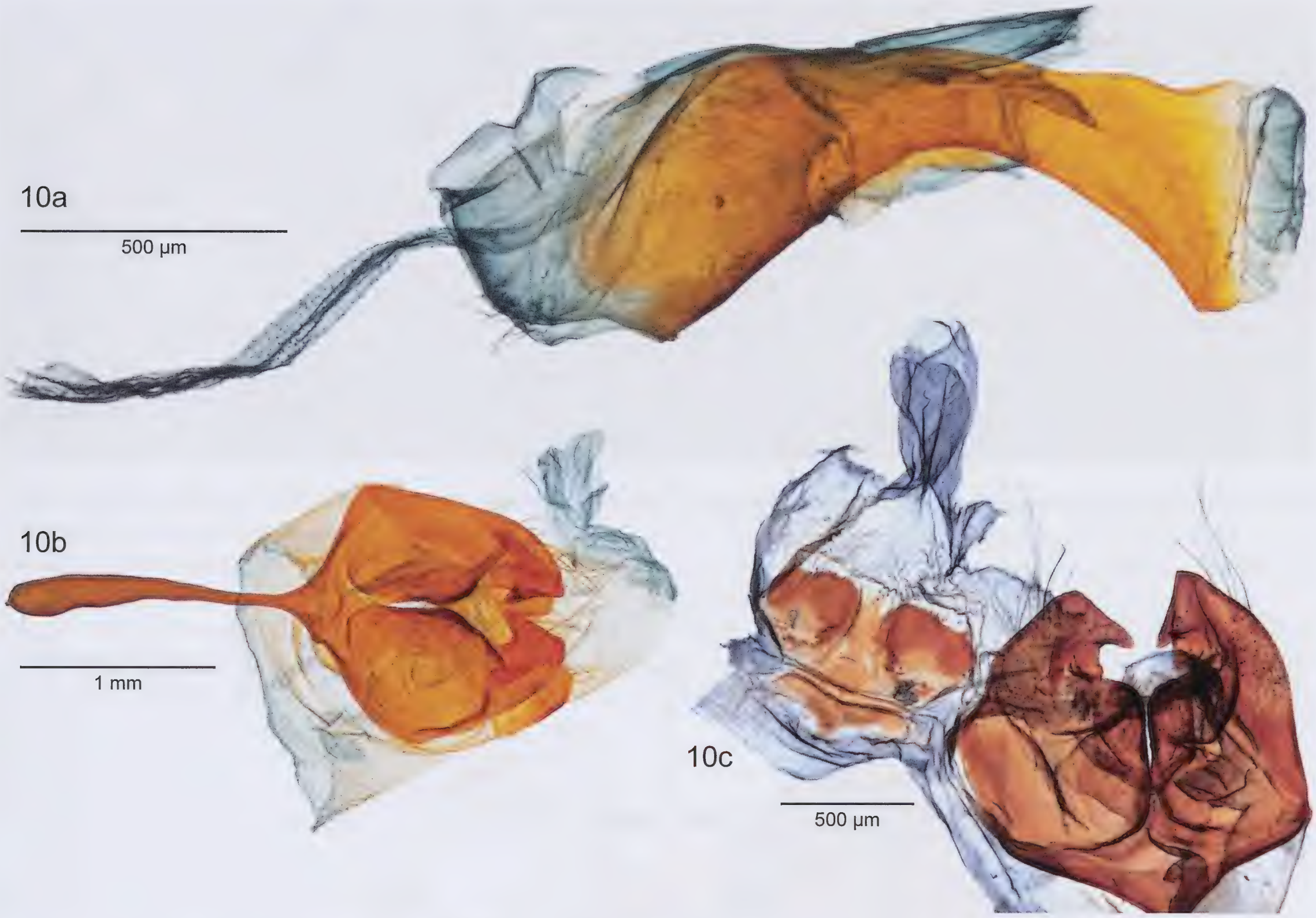


Fig. 10. Male genitalia of *Trichophiala devylderi*, (a) phallus and (b) genital capsule (specimen MHNG-ENTO-0013324), (c) part of genital capsule of specimen MHNG-ENTO-0013394 with tergites 9 and 10 spread out.

DISCUSSION

This study was prompted by the observation of numerous individuals of *Trichophiala devylderi*, both males and females, during a trip to Namibia in August 2017 and by the subsequent realization that very little was known about this species. The literature search conducted revealed in fact only the original description, dated 1879, by the Swedish entomologist Aurivillius, a second description by the same author in 1901 in a general review of the "Ethiopian genera of the family Striphnopterygidae" (synonym by Wallengren, 1858 of Eupterotidae Swinhoe, 1892 (Nässig & Oberprieler, 2007), a description by Gaede (1930), and very limited information available on websites, internet platforms and other sources. When the species is cited, a reference to the original description is usually presented with no details or new findings. As previously mentioned, only one photograph is available on two websites, that of the female type utilised by Aurivillius to describe the species, and two images of the female were found in the early literature (Figs 1 and 2). To our knowledge, no male image has ever been published. Likewise, male and female genitalia had never been fully analysed and described.

A comparative analysis of numerous adult specimens allows to conclude that two phenotypic forms of the species exist: a commoner form that has a sandy ground colour with a slight greyish suffusion and a less frequent form that has a darker rusty pink-brown colour and reduced or nearly absent darker suffusion on the hindwings. This observation prompted a detailed comparison of genitalia between the two forms. A slight difference in phallus was observed and this feature is a character of good taxonomic weight in this group of Eupterotidae. However, DNA barcode analysis revealed little genetic variation among the specimens processed and no difference between individuals of the two forms. This goes against the hypothesis of two distinct species and suggests instead that darker specimens represent mere individual variations from the more common and typical lighter phenotype. Additional molecular, morphological or ecological studies, as well as breeding experiments, might lead to a better understanding of the nature of these individual forms.

From a systematic perspective, *Trichophiala* is a monotypic genus. Its relationship with other members of the

Fig. 11. A female of *Trichophiala devylderi* (a) dorsal view, (b) ventral view. Vicinity of Korlia, Namibia, August 2017.

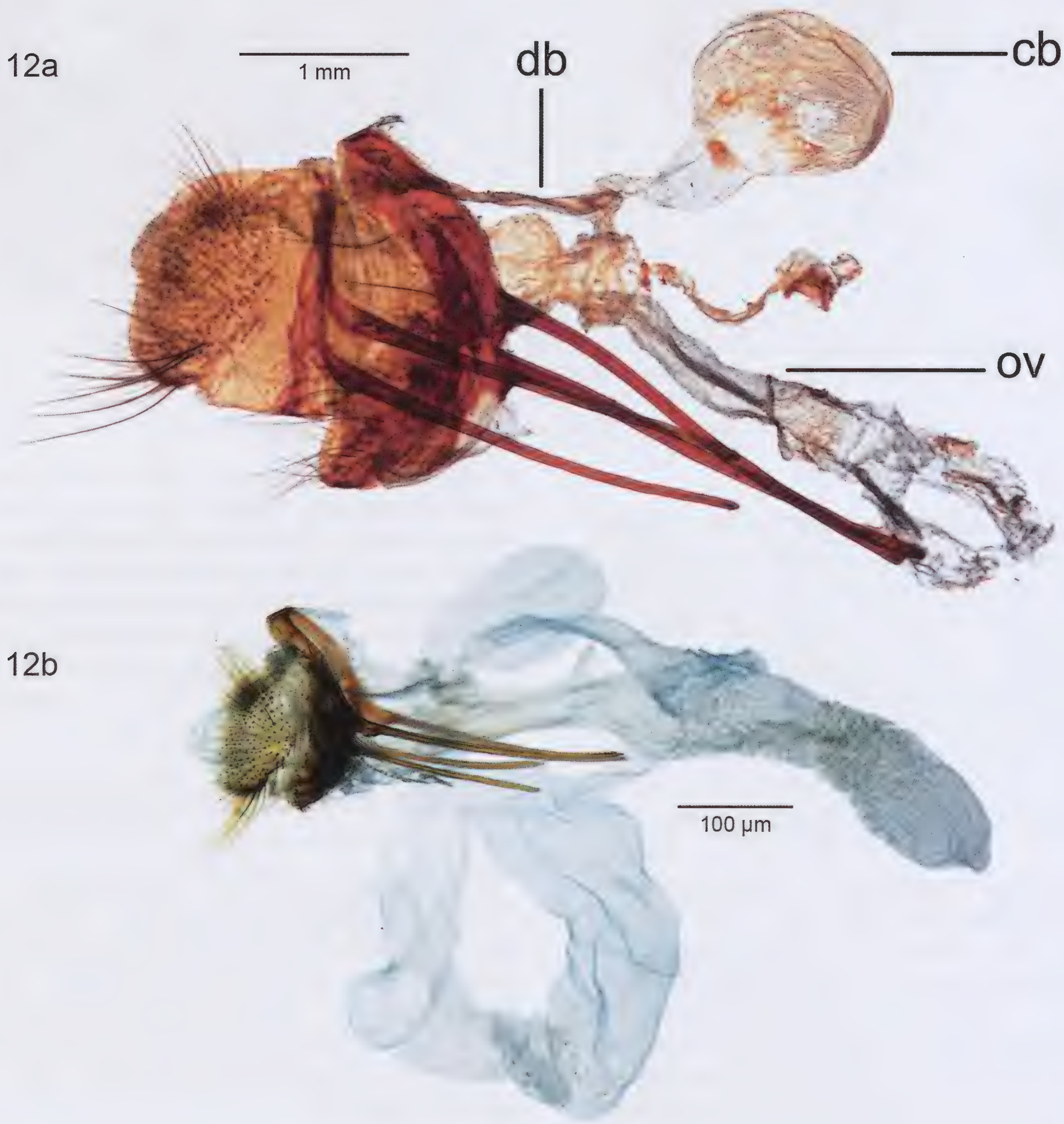


Fig. 12. Female genitalia of *Trichophiala devylderi*, (a) lateral view of specimen MHNG-ENTO-0013395 without glandulae sebaceae, (b) lateral view of lectotype (NHRS-SRAH000001507). db: ductus bursae; cb: corpus bursae; ov: oviduct.

Striphnopteryginae subfamily remains unelucidated, although DNA barcodes place it in close proximity of *Teratojana flavina* and general morphology and genitalia suggest, as already hypothesized by others, that *Trichophiala* may be closely related to *Phiala* and *Lichenopteryx*. The male genitalia are highly modified as in other members of the Striphnopteryginae (Oberprieler *et al.*, 2003). The gnathos is absent and the uncus present only as a pair of plates, without discernible posterior projections while the tegumen is interpreted here as a distinct narrow plate. The other male genital structures conform well to the diagnosis of the subfamily provided by Oberprieler *et al.* (2003). The female genitalia were not discussed by the latter authors.

Although this work has shed light on *Trichophiala devylderi*, much remains to be studied to have a comprehensive understanding of this taxon. Needed investigations include, for example, studies on its natural history: descriptions of the eggs, larva and pupa, as well as annual cycle, and parasites and predators. At the moment, these aspects are ignored. Equally poorly known is the larval foodplant although some reports point to the species feeding on acacia trees: in general, breeding Eupterotidae is reported as extremely difficult and only very few species have been reared so far given that the foodplant is unknown for most, and that numerous African species are specialist feeders (Vanhoudt, 2020-2021). Furthermore, the phylogenetic relationships of the genus with *Phiala, Lichenopteryx, Teratojana* and other Eupterotidae genera would greatly benefit from further molecular studies.

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